

Appendix B. Conceptual Ecological Models

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Introduction

A conceptual model is a narrative, table, and/or diagram that summarizes key components, influences, and processes in an ecological system. Like all multidisciplinary ecological monitoring programs, the Northern Great Plains Network (NGPN) is developing its long-term monitoring program based on an incomplete understanding of indicators and complex park ecosystems. Our incomplete understanding of park ecosystems is a primary reason why conceptual models are critical intellectual tools (Barber 1994; Noon et al. 1999; National Research Council 1995; Busch and Trexler 2003) in developing monitoring programs.

Conceptual models are intended to stimulate thought and discussion about which data we will collect, how this data will be interpreted, and what this information may mean to park management. The modeling process is a bootstrap approach for exploring potential monitoring priorities, for developing monitoring strategies that will meet our monitoring goals and objectives, and for improving our understanding of the systems (Starfield and Bleloch 1991). We start by describing what we know about the system, but quickly are led to integrate work of other scientists and managers to address limitations in our individual knowledge. This benefit is important particularly because ecological interactions transcend the disciplinary specializations of scientists designing monitoring programs (Allen and Hoekstra 1992). Models can be invaluable for enhancing communication among scientists, managers and the public. Modeling forces us to make transparent our assumptions about how the systems work and why we are focusing on specific monitoring objectives. This transparency makes it possible for scientists and managers to critique our assumptions and choices to help improve the monitoring program.

Use of Conceptual Models in the NGPN

In developing conceptual models, the NGPN initially developed a small set of models for assisting with selection of Vital Signs. These initial models focused on park stressors, bison-wildlife interactions, and grassland dynamics. Conceptual models subsequently have been developed as fundamental tools in exploring and justifying potential monitoring objectives for each Vital Sign. In this process, we first develop models, or adapt existing models, and focus on a single Vital Sign or sub-components of a Vital Sign. These models include summaries of major stressors of concern for the Vital-Sign resource, ecological processes models, and state-transition models. The models in this Appendix are not a completed suite of models, but rather are models we have completed as of early 2009 or have adapted from other I&M Networks (Table B-1). As we continue developing protocols, we will continue to develop more detailed conceptual models for each protocol, as well as models linking attributes across protocols, as an important step in refining our monitoring objectives. At the conclusion of this appendix, we provide a general overview of some general but concrete ways that NGPN conceptual models have affected our choice of Vital Signs and the initial stages of protocol development.

Throughout the development of the NGPN monitoring program, the Network seeks the following benefits from the conceptual-modeling process:

1. Formalize our current understanding of park ecosystems, including the context and scope of ecological processes operating at multiple spatial scales (Karr 1991).
2. Identify the primary current and potential stressors affecting these ecosystems, and describe the hypothesized specific impacts of these stressors, including intended and unintended consequences of management actions.
3. Identify key uncertainties in our understanding of ecosystems, interactions among components, and effects of drivers and stressors (including management actions).
4. Facilitate identification and prioritization of Vital Signs.
5. Help identify the specific measures that will be taken for each Vital Sign, monitoring objectives, target populations, and quantitative survey objectives.
6. Guide data collection and analyses by identifying important auxiliary variables, links among Vital Signs, and working hypotheses to be examined with specific analyses.
7. Strengthen links between monitoring results and park management, particularly by facilitating discussion of management thresholds in Vital Sign attributes.
8. Communicate and justify the ecological framework of this monitoring plan to a wide variety of audiences.

Table B-1. Primary developers of NGPN conceptual models.

Model	Model Developer	Narrative Developer
General model (Fig. B-1)	B. Gitzen	D. Licht and B. Gitzen
General stressor model (Fig. B-6)	B. Gitzen	D. Licht and B. Gitzen
Conceptual diagrams (Figs. B-7:B-10)	University of Maryland Center for Environmental Science and NGPN staff	B. Gitzen (brief narratives)
General grassland model (Fig. B-11) and fire/grazing/precip. model (Figure B-12)	J. Wrede (adapted from other sources)	J. Wrede (adapted from SOPN narrative)
Nutrient dynamics (B-13)	D. Licht; adapted from other source	D. Licht
State-transition Models (B-14:B-27)	B. Gitzen, with input from A. Symstad and D. Uresk	B. Gitzen; Mid- / Upper elevation Black Hills insect narrative by M. Bynum
Exotic detection (B-28)	M. Bynum, adapted from other sources	M. Bynum
Prairie dogs (B-29)	J. Wrede	J. Wrede
Bison/other wildlife (B-30)	D. Licht	D. Licht
Cave resources (Tables B-2:B-6)	M. Bynum, JECA/WICA staff, B. Gitzen	M. Bynum
Aquatic drivers/stressors (Fig. B-31)	Joyce Williamson and Barbara Rowe, USGS South Dakota Water Science Center	M. Wilson
Stream/river ecosystem model (Fig. B-32)	Scott et al. (2005) and NPS (2005b)	M. Wilson
Aquatic indicators and measures (Table B-7)	Joyce Williamson and Barbara Rowe, USGS South Dakota Water Science Center	M. Wilson

General Ecological Model

To help organize more detailed models, we developed a simple overall model to categorize major ecosystem components and to show the dominant influences on all Network ecosystems (Figure B-1). In this section, we provide a general overview of these major influences.

This general model highlights several issues relevant to all finer-scale models:

- a) Ecosystem biotic characteristics are driven both by abiotic factors that are largely external to parks and operate at much larger spatial and temporal scales (driver, or external forces that have large-scale influences), and by biotic and abiotic interactive controlling factors that are part of the ecosystem rather than external to it (Jenny 1941; Chapin et al. 1996). Drivers determine what type of ecosystem can form in a place (Dale et al. 2000), and constrain processes such as energy flow. Disturbance regimes and other overriding influences both affect and are modified by other ecosystem elements (Chapin et al. 1996).
- b) Stressors are human–caused perturbations or those that are natural events but applied at excessive or deficient levels (Barrett et al. 1976:192). Defining important Network stressors and potential impacts of these threats has been a primary emphasis in the development of the NGPN monitoring program.
- c) NGPN parks support managed ecosystems. Improving this management is an ultimate goal of the monitoring program. (Noon et al. 1999).

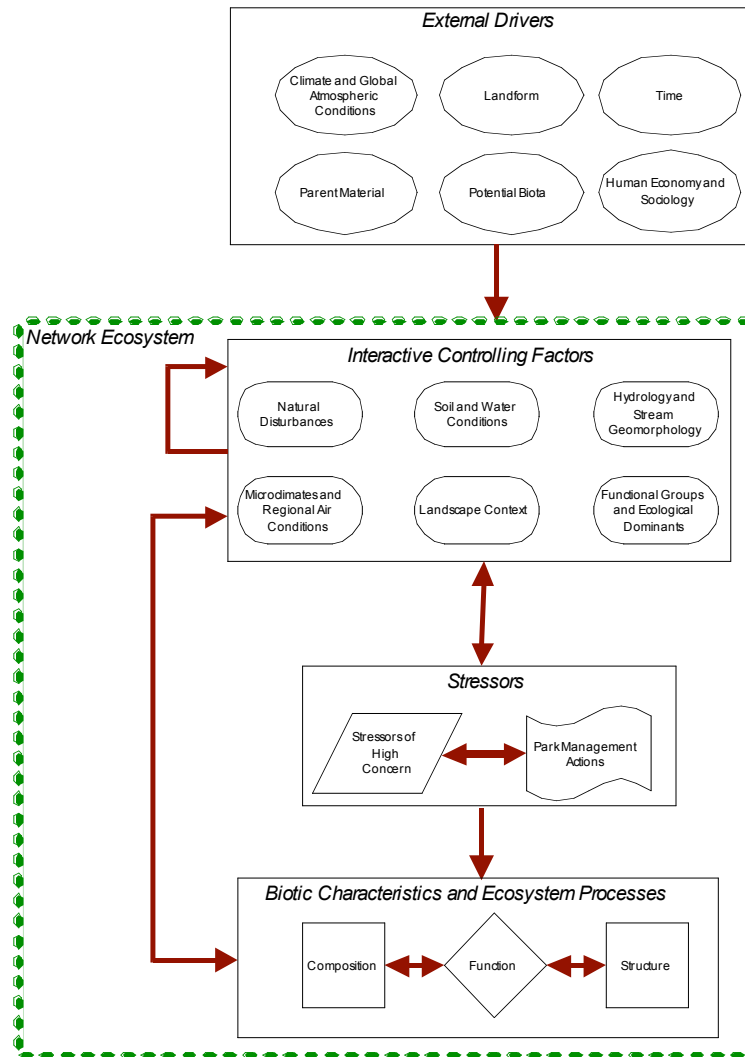


Figure B-1. General model for factors shaping ecosystems in the NGPN.

Drivers and Interactive Controlling Factors in the Northern Great Plains

The general ecological model for the Network emphasizes the major controlling influences on park ecosystems. External drivers include global climate and atmospheric conditions, parent material, landform, potential biota, time, and large scale sociological and economic factors. Interactive controlling influences are abiotic or biotic components of an ecosystem that broadly affect and respond to other components and processes in the system. These include natural disturbances, soil and water conditions, hydrology and river geomorphologic characteristics, microclimates and regional atmospheric conditions, the landscape context of the ecosystem, and species or species groups with uniquely large effects. In the following section, we discuss how selected drivers and controlling factors shape NGPN ecosystems, focusing primarily on grasslands.

Climate: Great Plains weather is highly influenced by the clashing of air masses from westerly winds that are modified by arctic airstreams from the north and tropical airstreams from the south. This mixing produces results in variable weather, particularly in the summer. Westerly air masses that become saturated over the Pacific Ocean become obstructed by the Rocky Mountains, which causes precipitation over the mountains and drier conditions on the leeward side of the mountains. These drier conditions result in the short to mid-grass ecosystems of the northern and western plains regions. As these air masses continue across the broad flat plain they increase in temperature and can hold more moisture. These westerly winds can then collide with arctic and tropical masses and result in stormy, unstable climatic summer weather conditions. The clashing of air masses provides more rainfall which supports the mixed-grass of the central Great Plains, and still more rainfall for the tall-grass prairie of the eastern plains.

The Northern Great Plains is characterized by extremes in weather ranging from hot dry summers to cold winters with prolonged snow cover (Figures B-2, B-3). High winds compound the effects of temperature and precipitation. Annual variation is great, with drought cycles returning approximately every decade. Borchert (1950) summarized the common climatic attributes of North American prairie as 1) low winter snow and rainfall, 2) high probabilities of large rainfall deficits in summer (as it relates to primary production), 3) fewer days of rainfall compared to nearby forested areas, 4) low summer cloud cover, 5) low summer relative humidity, 6) large departures from average temperature, 7) frequent hot, dry winds in summer; and 8) frequent departures from average climatic conditions. Spatial and temporal variation in precipitation has fundamental effects on ecosystem properties in the NGPN (e.g., Figure B-4). The variable weather in the Northern Great Plains can confound analyses of changes in the ecosystem and the causative factors of those changes. To overcome this, ecosystem monitoring should be accompanied by local weather data.

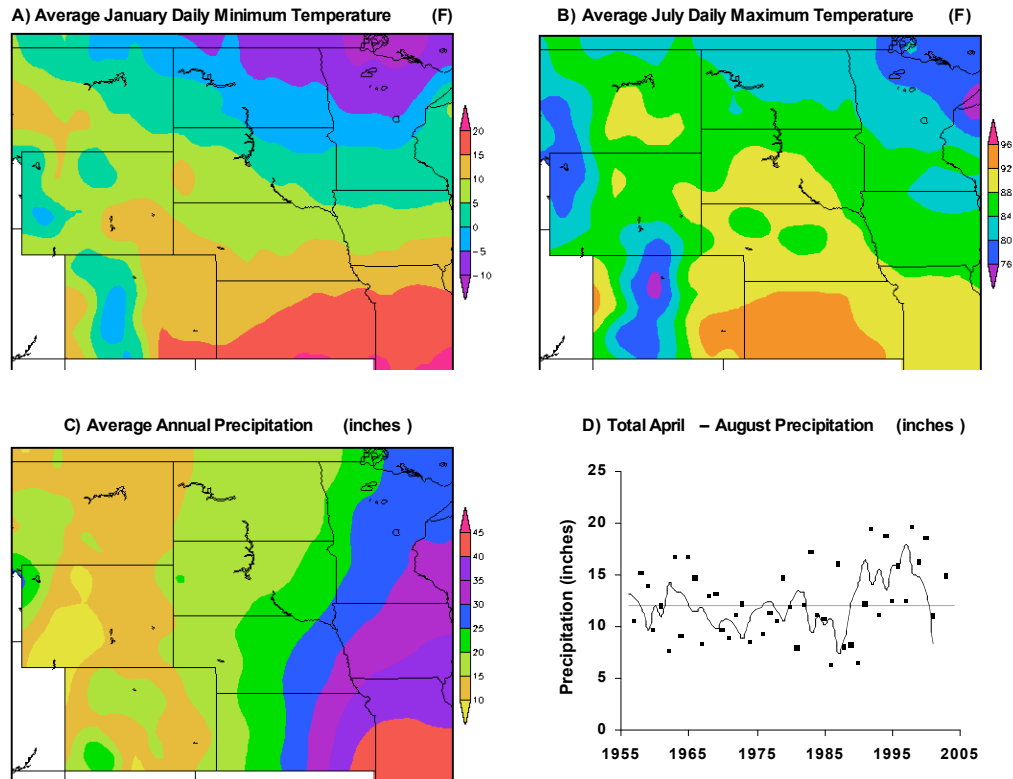


Figure B-2. Climatic summaries for the NGPN.

A)-C) Average temperature and precipitation for the U.S. Northern Great Plains and adjacent regions, 1961-1990. D) Total growing-season precipitation (squares) and smoothed trend (black line; 3-year moving average), 1956-2005, near Badlands NP (Interior, South Dakota). Years with > 2 missing daily totals in 1 or more months are omitted (1975 and 2002). Gray line is the average for this period. A)-C) and data for D) from High Plains Regional Climate Center, University of Nebraska, Lincoln (HPRCC 2007).

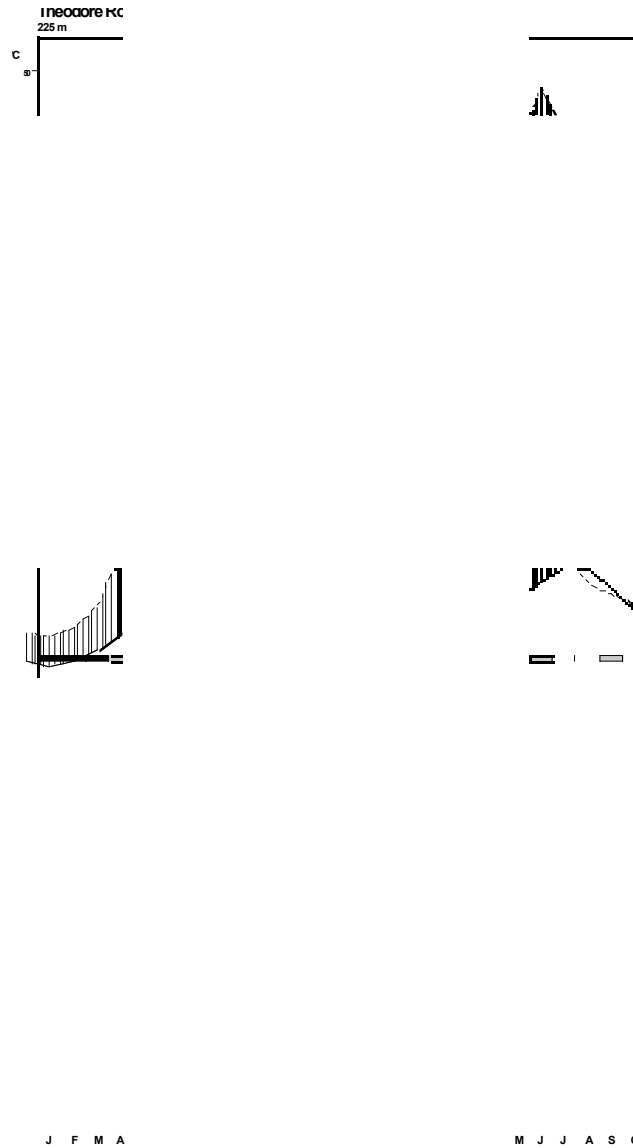


Figure B-3. Climate diagrams (Walter and Lieth 1960) of selected locations in the Northern Great Plains Network.

In each figure, elevation and average annual precipitation are listed on top. The solid line is the average monthly temperature (C). The dashed line is average monthly precipitation (mm). The area between the two lines is dashed except during periods when the temperature line is higher than the precipitation line, corresponding to average peak drought periods. The horizontal bar summarizes the frost season: black shading indicates months where average minimum temperature is below 0 C; gray indicates months with extreme lows < 0 C; empty portions of the bar indicate months with no recorded freezing temperatures. Data were accessed from the High Plains Regional Climate Center (2007). For Mount Rushmore NM, data are from 1962-2005. For other parks, data are from nearby towns with data for 1948 (1949 in Badlands NP) through 2005. Figures were constructed with a function modified from package ‘climatol’ (Guijarro 2006) in program R.

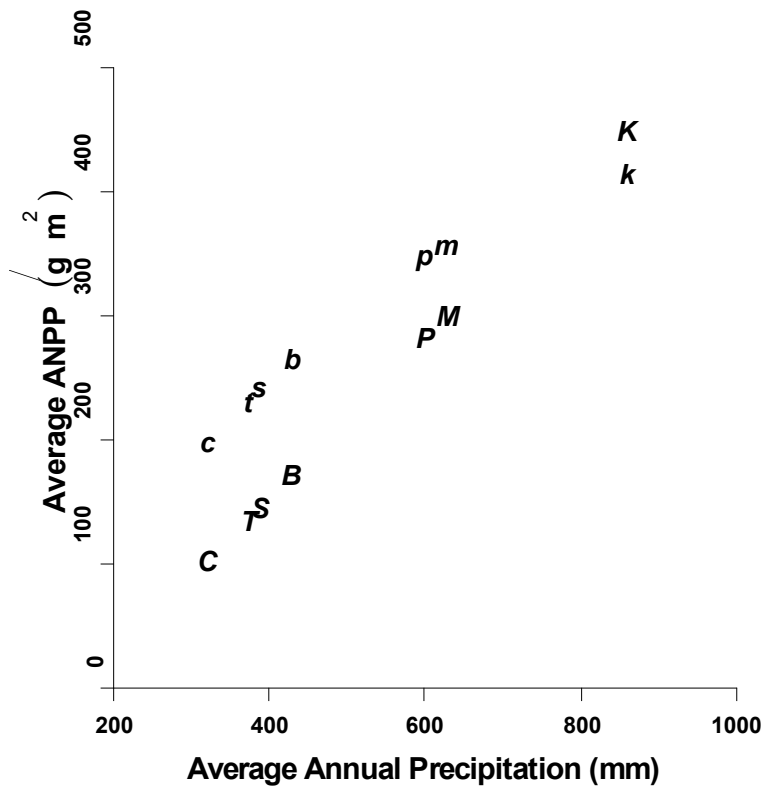


Figure B-4. Predicted aboveground annual net primary productivity for selected NGPN parks and other shortgrass and tallgrass prairie sites adjacent to the Network.

Upper case letters are predicted values from ANPP/precipitation linear regression developed by Milchunas and Lauenroth (1993) for 127 grassland sites worldwide. Lower-case letters are predicted values from exponential relationship developed by Webb et al. (1978) for 7 grasslands in the western U.S. Symbols: C = Shortgrass Steppe LTER (CO), T = THRO, S = SCBL, B = BADL, P = Pipestone National Monument (MN), M = MNRR, K = Konza LTER (KS).

Landform: Much of the Great Plains is relatively flat. However, even in this region, landform could be considered the driver among drivers. The Rocky Mountains are the primary reason the Northern Great Plains are dry and the location in the middle of the North American continent is the reason the region experiences a temperate climate. Yet even at a much smaller scale, landform affects park resources and processes. For example, at Theodore Roosevelt NP, north facing slopes often support solid stands of juniper whereas south facing slopes may be mostly barren. The presence of bighorn sheep at Theodore Roosevelt and Badlands NPs is a direct consequence of the topography. The Niobrara River Valley supports a diversity of plant communities whose occurrence is determined by landform, as well as hydrology, parent material, disturbance, and historical biogeography (Figure B-5).

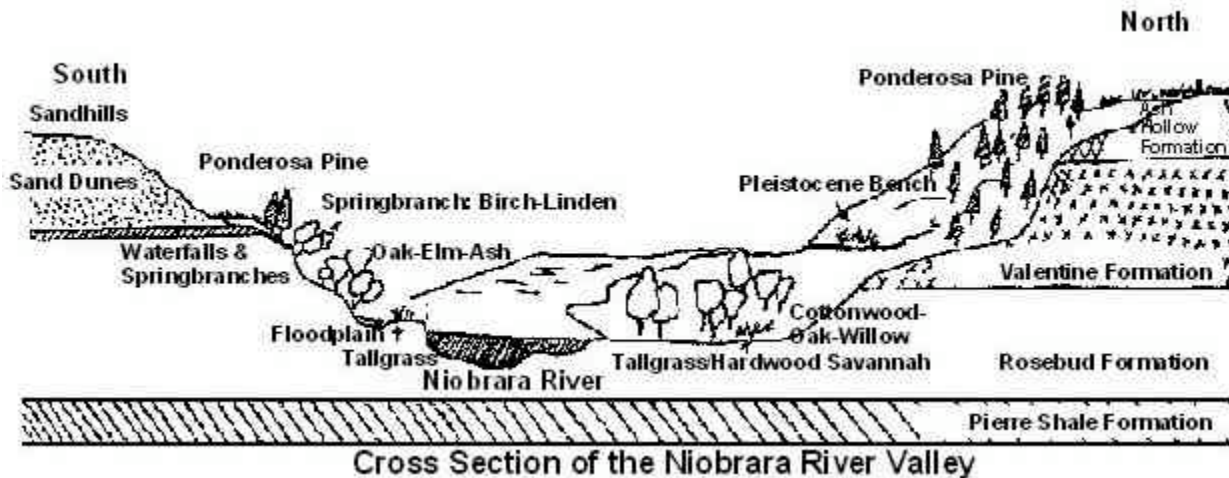


Figure B-5. Landform, geology and plant communities of the Niobrara River Valley.
Figure drawn by Ed Heinert for the Nature Conservancy.

Parent Material and Soil Characteristics: Soil is the result of complex and long interactions between climate, fire, hydrology, bedrock, and biota. Prairie soils were formed primarily from sediment washed down from the Rocky Mountains and the Black Hills, mixed with rubble from glaciers, and windblown sand, silt and clay. This combination results in nutrient-rich, deep soils in many areas of the NGPN that are some of the most productive on earth. Grassland soils are fundamentally different than forest soils (Simms 1988). Forested areas generally contain 20-50 tons of topsoil per acre, while an acre of mid-grass prairie can contain as much as 200 tons per acre. Soil formation is a slow, continuous process. About 1 inch (2.5 cm) of new topsoil is formed every 100 to 1,000 years, depending on climate, vegetation and other living organisms, topography, and the nature of the soil's parent material (Sampson 1981). Prairie soils are generally nitrogen and carbon poor, although there is wide variability. Prairie soils are often nitrogen limited, affecting vegetation composition and vigor at a site (Seastedt 1995). Soil nutrient transport is generally slow; however, fire and grazing (especially under historic patterns) can cause rapid pulses of transport. Other soil characteristics such as physical composition, moisture levels, biota, and chemical composition also influence the primary productivity at a site. Where evaporation is low, water is more likely to remain in the soil, increasing the rate of mineral weathering and allowing large amounts of nitrogen, phosphorus, and sulfur to accumulate in conjunction with carbon.

The physical characteristics of soil can directly affect animals such as prairie dogs, a species that is known as an ecosystem engineer and one that has direct impacts on soil characteristics. Prairie dogs need soils that can maintain and support their burrowing. Large areas of the Great Plains such as the Nebraska Sandhills are void of prairie dogs because the sandy soils do not support burrowing.

As Europeans moved west, native prairie began to be converted to cultivated agriculture as early as the 1850's (Peterson and Cole 1996). When prairie is converted to row crop agriculture, the mixing and grinding of farm tools reduces surface cover and destabilizes soil structure by reducing aggregate size. In addition, organic carbon loss is accelerated by agriculture, and cultivated crops return little carbon to the soil. The early farming practices did very little to capture and retain moisture. The Dust Bowl of the 1930's, resulted in the removal of much of the Great Plains protective vegetative layer and exposed vast areas of cultivated prairie soil to wind action and drought (Sampson 1981). In addition, chronic heavy grazing by livestock can compact soils and affect many of their characteristics and functions (e.g., water infiltration). Several NGPN parks contain tracts of formerly cultivated land that are in various stages of restoration.

Fire: Fire is critical to creating and maintaining temperate grasslands. North American prairie fires historically occurred in all months of the year, but fuel conditions and weather patterns lead to peak fire frequencies in July/August and a secondary peak in the spring (Bragg 1982). Native Americans frequently ignited fires to drive or attract game. In the comparatively humid tallgrass region fires may have historically occurred every 3-10 years. In mixed-grass prairies fires were probably a more regular occurrence, sometimes striking in both the spring and fall at the same site (Bragg 1982). In the shortgrass regions fires occurred less frequently (due to a lighter fuel load), perhaps only every 15-30 years (Wendtland and Dodd 1992). The effect of fire is variable. For example, in mixed-grass prairies both dormant-season and growing-season burns generally decrease total plant production in that year, while in tallgrass prairie, mid- to late-spring burning generally increases overall productivity (Bragg 1995).

Fire results in substantial losses of nitrogen through volatilization, with perhaps twice as much nitrogen lost in a single fire as enters the system yearly in rainfall or by nitrogen-fixing organisms (Seastedt 1988; Ojima et al. 1990; Hobbs et al. 1991). The removal of vegetation and plant surface litter also results in an exposed soil surface that is typically warmer and drier than that of unburned prairie. With enhanced plant growth, available nitrogen is locked away in plant tissue, while higher photosynthetic rates place strong demands on soil water. Plants respond to nitrogen and water limitations by allocating more photosynthate to roots. This input of new roots to prairie soil is critical to the accumulation of soil organic matter and humus (Seastedt 1995). The subsequent improvement in forage following a fire attracts bison and other ungulates. Conversely, grazing patterns affect the patchiness and intensity of fires, and both interact with climate, a major driver of grassland ecosystems (Anderson 1982).

Ecologically Dominant Species: Grassland systems are shaped by grazers (Milchunas et al. 1988). Grasslands generally support large numbers of herbivores, including large concentrations of nomadic ungulates that shape grassland systems (Detling 1988; Licht 1997a). Worldwide, large mammalian herbivores (including livestock) remove, on average, 30 to 40% of the aboveground net primary production in grasslands, while insects remove another 5 to 15%. Belowground invertebrate consumers, primarily nematodes, consume another 6 to 40% of the belowground net primary production. The plant species composition of grassland can change in response to herbivory. As a general statement, Northern Great Plains species such as big

bluestem, little bluestem, and Indian grass decrease under regimes of prolonged grazing while species such as blue grama, side-oats grama, and buffalograss increase. Ungulate grazers increase nitrogen cycling in grasslands and are likely to affect export rates as well (Blair et al. 1998).

However, the impacts of herbivory can differ from one site to the next and also interact with fire and climate. Chronic heavy grazing by ungulates may result in a loss of root mass, as plants respond to herbivory by using root reserves to produce new foliage, rather than sending photosynthate to the root system to find new sources of N and water. In the western portions of the prairie, this system may prevail, with the dominant species well adapted to grazing. Infrequent grazing may function similarly to infrequent fire, causing a transient pulse of productivity in response to increased availability of nitrogen, water and light. Landscape heterogeneity due to grazing (and fire) is an important characteristic of grassland ecosystems, and responsible for much of the biological diversity. Monitoring of beta (i.e., among site) diversity can be an important measure of the health and diversity of grasslands. Whereas heavy and prolonged grazing may be detrimental to many plants (i.e., the *decreasers*) and animals (e.g., many butterflies, game birds) within grassland landscapes, others benefit. For example, in portions of the Northern Great Plains prairie dogs, swift fox, ferruginous hawks, and mountain plovers all benefit from heavy grazing by ungulates. From an ecological perspective, the terms “over-grazing” and “under-grazing” are only useful relative to some desired baseline grazing level and its effects on particular elements or processes of the grassland ecosystem.

Hydrology and Water Characteristics: The hydrology of any particular site in the Northern Great Plains is closely tied to precipitation; however, in some cases it may be precipitation that occurred either in a faraway place (e.g., rivers) or time (e.g., groundwater). Great Plains hydrology is widely recognized as a limiting factor for both wildlife and people (see Longo and Yoskowitz 2002). Water stresses the Great Plains ecosystem not only because of its scarceness, but also because of its variability both temporally and spatially. This variability (in terms of availability) is generally more pronounced away from the Black Hills and Rocky Mountains. Many species adapt to this variability by senescence, movement, torpor, or other means. Conversely, anthropogenic increases in water availability can jeopardize grassland ecosystem integrity by allowing invasion of species that may outcompete native species.

Prairie streams and rivers are characterized by variable flow regimes (Matthews 1988; Dodds et al. 1996). In low-order prairie streams, surface water is often ephemeral and intermittent for any particular reach. Low-order streams typically alternate between high flows in spring and early summer to intermittent flows to dry conditions during late summer and winter. Prairie rivers often have wide fluctuations in surface area with extensive exposed sand and mud flats in the summer and fall. Scouring floods may interrupt stream and river flow at any time, but are most prevalent in association with spring and summer storms (Gray et al. 1998). The natural hydrograph of the Missouri River differs from most other streams in the region in that it typically has two regular peaks; an early spring rise (from snowmelt in the prairie combined with rainfall) and a late spring rise (from mountain snowmelt at higher elevations; Hesse and Sheets 1983).

Many first- and second-order streams in prairies occur in areas devoid of trees. The lack of vegetative inputs (i.e., leaves and woody debris), combined with frequent and prolonged dry periods and periodic scouring floods, allow for very little in-stream decomposition (Matthews 1988). Therefore, entire groups of stream detritivores are missing from prairie streams. The organisms present are adapted to the extreme variability in prairie stream ecosystems. They tend to have stress-resistant life stages, short generation times, rapid growth, rapid colonization potential, or combinations of these traits (Matthews 1988, Gray and Dodds 1998). The high exposure of prairie streams to sunlight results in within-stream primary production being a major source of organic matter; however, such production may be limited by organic carbon (Gray and Dodds 1998). In contrast, allochthonous inputs, especially leaf litter, predominate in the few forested streams in the Network and in-stream primary production is low. Macro-invertebrate communities can be a good indicator of aquatic nutrient pathways as well as many other variables.

Stressors of Ecosystems of the Northern Great Plains Network

An alternative version of the Network's general ecological model (Figure B-6) emphasizes the major categories of stressors affecting Network parks, and the general scale at which these stressors operate. Expanded versions of this stressor model focus in more detail on specific impacts to vegetation (Chapter 2) and caves (this Appendix).

Figure B-6 illustrates the major management actions taken by NGPN parks, and the stressors targeted by each management activity. Regional changes in climate and atmospheric conditions, water quality and hydrology, and amount of natural habitat in the surrounding landscape are largely or completely outside of park management control, even though these changes may have huge impacts on park ecosystems. Most other stressors are also broadly affecting the regional ecosystem of the Northern Great Plains (e.g., fire suppression); their effects on park ecosystems can be reduced through management actions. However, these stressors will continue to operate at the regional scale; park management can reduce effects but not eliminate the causes of these stressors.

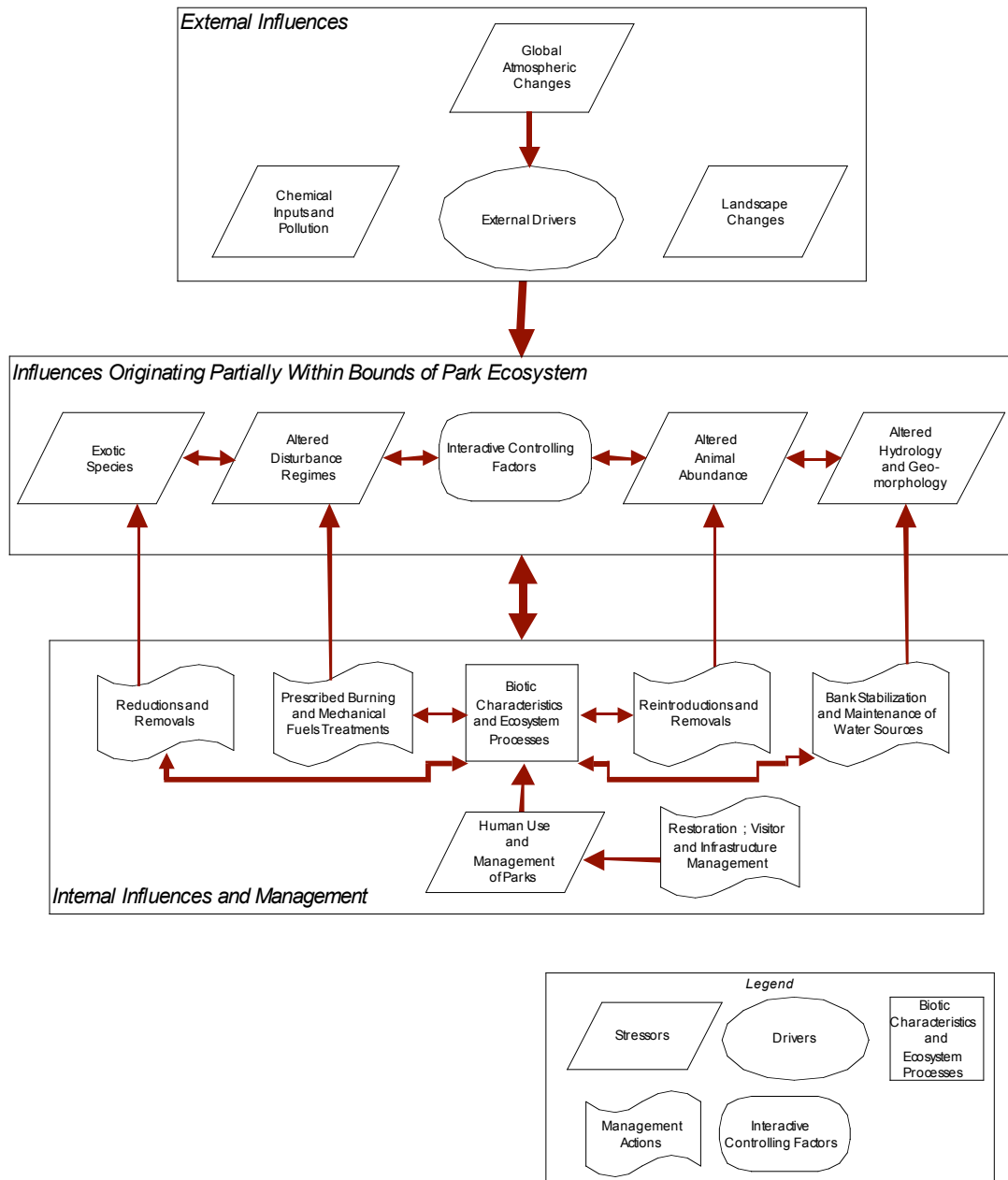


Figure B-6. Alternate general ecological model for the NGPN.

This version emphasizes major stressors affecting Northern Great Plains park ecosystems and management actions targeting these stressors.

The list of stressors to Northern Great Plains parks is generally consistent with the list of stressors to savanna ecosystems globally, i.e., land use change, elevated CO₂, increased nitrogen deposition, climate change, and alien biota (Sala et al. 2000). A discussion of the various stressors follows.

Global Atmospheric Change: Anthropogenic climate change could affect weather patterns in the Great Plains by increasing temperatures (especially in summer) and precipitation (National Assessment Synthesis Team 2000). However, soil moisture may decrease due to increased evapotranspiration. A warmer Great Plains could result in a shift to more C₃ (i.e., cool season) plants because these plants can better exploit soil moisture in the spring before the water deficits of summer (Clark et al. 2002). However, other analysis suggests a change to more C₄ plants (Collins and Glenn 1995). Climate change may affect not only the means, but the variability in weather patterns, perhaps resulting in longer drought cycles. A modeling study of potential climate-change effects at Wind Cave NP found that global warming could increase grassland vegetation and decrease forested and shrubby vegetation (Bachelet et al. 2000).

Altered Disturbance Regimes: Fire suppression in the Black Hills and eastern portions of the NGPN, has led to encroachment of woody species affecting the composition and form of grassland ecosystems. Misapplication of fire may stress a system as well. For example, prairie fires in the presence of grazers such as bison typically burn in a patchy pattern. Such pattern leaves refugia for small invertebrates and provides landscape heterogeneity. In contrast, fires in the absence of grazing can reduce landscape diversity and even extirpate species.

Altered Hydrology and Geomorphology:

Dams and altered hydrology: Most rivers and streams in the Northern Great Plains are dammed. Even tiny ephemeral drainages are often dammed for purposes of livestock. The largest river in the region, the Missouri, is one of the most dammed and altered rivers in the country. Approximately 36% of the river has been inundated by reservoirs, 40% has been channelized, and the remaining 24% has been altered and degraded by the patterns of water releases from the six major dams on the river (U.S. Fish and Wildlife Service 1993). The impacts of dams include changes in sediment transport, geomorphologic processes, water levels, flow rates, groundwater hydrology, water temperature, oxygen levels, fish movement, floodplain composition and structure, and many others. Dams are a severe stressor of park resources at Fort Laramie NHS, Fort Union Trading Post NHS, Knife River Indian Villages NHS, the Missouri NRR, the Niobrara NSR, and Scotts Bluff NM.

Groundwater and Irrigation Withdrawals: Groundwater and surface water withdrawals for irrigation, livestock, and domestic use threaten not only the aquatic ecosystems within the grassland biome, but also Great Plains society. Luckey et al. (1988) predicted that at the current rate of water depletion parts of the plains could face extreme water shortages by the year 2020, resulting in dire economic and social consequences. Groundwater and irrigation withdrawals affect all Network parks, although the degree of the impact does not appear severe in most cases.

Canal seepages: Irrigation canals at Scotts Bluff National Monument and Fort Laramie NHS can increase availability of moist soils capable of supporting riparian vegetation.

Chemical Inputs and Pollution:

Air Pollution: The Great Plains has typically been known for its clear skies and clean air. However, air pollution may increase in Network parks due to energy development in Wyoming and Montana. Increased atmospheric nitrogen associated with air pollution may threaten the stability of tallgrass prairie remnants (Wedin and Tilman 1992); nitrogen fertilization may alter vegetation composition in more widespread ecosystems of the Network.

Water Pollution: Physical pollution can occur as the result of land use practices such as logging that increase sedimentation into streams and rivers. Chemical pollution can take a variety of forms, including point pollution and non-point pollution, of pesticides, industrial waste, and atmospheric deposition. Biotic pollution includes fecal material and other organic inputs. This is a common concern in the Northern Great Plains because much of the landscape is used for livestock. Nutrient loading ultimately favors eutrophic species and can dramatically change community composition. Selenium is a natural mineral that is released by irrigation practices; elevated levels of the element have been found in addled piping plover and least tern eggs in Nebraska (Fannin and Esmoil 1993) and South Dakota (Ruelle 1993).

Pesticides: Perhaps more than 200 million pounds of pesticides are applied annually in the Great Plains (Licht 1997a). The impacts of herbicides, insecticides, fungicides, and other pesticides on wildlife are well documented in the scientific and popular literature. Pesticide impacts in parks may be the result of park control efforts (e.g., herbicides for controlling exotic plants) or from external applications.

Landscape Changes: Although the impacts of fragmentation have been known since the early days of wildlife management, only in recent years have scientists fully understood the extent and implications of this stressor (Saunders et al. 1991; Turner et al. 2001). At a regional level, the fragmentation of the Great Plains has had numerous harmful impacts on the region's biological diversity (Licht 1997a; Engle et al. 2003). The effects of fragmentation are especially severe when adjoining land use differs dramatically from the protected area. For example, nest predation and parasitism of grassland birds are higher near a grassland/woodland edge than they are away from the edge (Burger et al. 1994). Similar impacts occur when the grassland edge abuts cultivated fields or residential areas. Saunders et al. (1991:2) stated that small fragmented tracts of habitat are often "predominantly driven by factors arising in the surrounding landscape." In the case of small prairie parks, the remnant tract may look like grassland, but many of its ecological processes may be driven by the adjacent habitat. Fragmentation also disrupts movement patterns that were often critical to the life history of grassland species. Without connectivity between suitable patches, many species cannot survive stochastic and catastrophic events. All parks in the Network suffer from this stressor, although to varying degrees. The stressor is especially severe at small parks located in a dramatically altered landscape, such as Fort Laramie NHS, Fort Union Trading Post NHS, Knife River Indian Villages NHS, the Missouri NRR, and Scotts Bluff NM.

Although fragmentation and the small size of parks are typically inseparable factors, there are impacts and stresses on a system that are more strongly associated with area, regardless of adjoining land uses. The loss of species from small habitats is reflected in the well documented species-area relationship of island-biogeography, which states that the number of species found in a habitat island is a function of its area; i.e. the larger the island the more species it can support (MacArthur and Wilson 1967). This relationship is most readily apparent with large mammals such as wolves, bears, and mountain lions that simply need large areas to meet their biological needs. However, it is also relevant on much smaller tracts. For example, many grassland birds are area-dependent during the breeding season and simply won't breed without adequate area. Samson and Knopf (1982) found that in the tallgrass region only relict prairies larger than 395 acres were able to maintain stable bird communities and that the annual number of prairie bird species was more strongly correlated with area than it was with habitat heterogeneity, edge, or isolation. Herkert (1994) found that the savanna, grasshopper, and Henslow's sparrow, bobolink, and eastern meadowlark required minimum areas ranging from 12-136 acres for breeding purposes.

Generally speaking, about two-thirds of all grassland bird species appear to be area-dependent during the breeding season; in contrast, many alien bird species that are increasing to pest-like proportions in the Great Plains are area-independent (e.g., starling, common grackle, house sparrow). In some cases a small site may not have all the resources a species needs to survive such as water, shelter, or breeding areas. Although management could theoretically create the habitat diversity and features needed, this creates a dilemma because it would have to be at a tradeoff of smaller habitat patches which theoretically makes the site unsuitable for area-dependent species.

Even when a site is large enough to support a species, it may not be large enough to maintain genetic variability or natural behaviors and processes. For example, inbreeding and a lack of genetic variability is a concern for bison, bighorn sheep, and black-footed ferrets in Network parks. Another problem with small park size is that it reduces the ecological redundancy that was characteristic of the pre-Columbian Great Plains. Without redundancy in habitats there may be no refugia for species to persist through catastrophic events (e.g., fire). Many grassland species historically survived catastrophic events by re-colonizing disturbed sites, but such refugia may not be present on small sites. For example, prescribed fires ostensibly set for prairie management that did not leave nearby unburned areas have likely extirpated butterflies from many small prairie tracts (Swengel 1996). Without redundancy there is little margin for error in terms of management action. All parks in the Network suffer from their small size, but the impact is especially severe at eight of the parks. The stress is exacerbated at many parks, including large units such as Badlands NP, by the linear and irregular shape of the parks which decreases the area to perimeter ratio.

Human Use of Parks and Management:

Roads: Roads have many obvious impacts on a park ecosystem, such as noise disturbance and mortality. Mortality can be especially high for scavengers such as swift fox and species that may

find ideal perches (utility poles) near the roads and prey on the road (e.g., loggerhead shrikes feeding on grasshoppers). Roads can also have less observable effects. For example, they can also serve as barriers to some species (e.g., Swihart and Slade 1984).

Visitor Impacts: Visitors to park units can directly impact park resources. For example, trampling of vegetation and compaction of soils is a concern at several parks (e.g., on the Tower at Devils Tower NM). Trail erosion due to hikers is an impact at other parks (e.g., Mt. Rushmore NMEM). Some wildlife species, including many raptors, large ungulates, and carnivores, are sensitive to human disturbance and will avoid areas with high human presence. Human impacts can also be indirect. For example, picnickers on Missouri and Niobrara River sandbars leave food remains which attract predators such as magpies and common crows, resulting in reduced nest success of rare sandbar-nesting birds such as the piping plover (Licht and Johnson 1992). Visitor impacts occur at all parks although the severity of the impact often differs greatly within parks.

Infrastructure: Buildings, maintenance areas, and other infrastructure are for park operations. This infrastructure directly eliminates natural resources and habitat, and may lead to increases in fragmentation and other stressors. The amount of infrastructure in Network parks ranges from about 7% of the land cover to less than 1%. The percentage of land cover in administrative areas is generally inversely correlated with the total acreage of the parks.

Prior Land Use: Restoring previously disturbed areas can be very difficult. For example, formerly cultivated areas have a degraded soil structure with the various horizons homogenized into uniform strata. In many cases they may have significantly reduced levels of organic matter. Formerly cultivated and disturbed areas are prone to invasion by exotic plants, so the stressor works in combination with others. Parks with significant acreages of formerly cultivated areas include Fort Laramie NHS, Fort Union Trading Post NHS, Knife River Indian Villages NHS, Missouri NRR, and Scotts Bluff NM.

Miscellaneous: Several other stressors affect park resources to varying degrees. Noise disturbance from aerial overflights and other activities has the potential to disrupt wildlife behavior, as well as visitor experiences. Structures and development outside a park can also affect visitor experiences. The impacts become especially dramatic in the park units that are comparatively more pristine and not yet affected by viewshed impacts.

Exotic Species:

Exotic Plants: Nationwide, exotic plants rank as the greatest threat to the ecology of our National Parks (Hester 1991). The impacts of exotics are manifold. Most noticeable is that they can completely displace native flora. This is especially likely to happen in disturbed areas because most plants native to the Great Plains are not good colonizers. The change in vegetation community has a ripple effect throughout the system. Every park in the Network suffers severely

from this stressor. Notable exotic plants in the Northern Great Plains include crested wheatgrass, purple loosestrife, spotted knapweed, leafy spurge, Canada thistle, sweetclover, several species of brome grass, Russian olive, and wormwood.

Exotic and Feral Animals: Whereas exotic plants rank as the greatest threat to the ecology of our National Parks, exotic animals were the fourth most commonly reported problem (Hester 1991). Feral animals including dogs and cats are widely recognized as having severe impacts on some wildlife resources. The impact of feral animals is closely correlated with nearby human population density. Many exotics, such as house sparrows, house mice, and starlings are also strongly associated with human presence. Plague is an exotic to North America that can affect both people and wildlife. However, the impacts of introduced animals also include species native to North America, but alien to the park and region. For example, raccoons, opossums, and crows have all greatly expanded their range due to anthropogenic changes to the landscape. These species can have severe impacts on species native to a site such as grassland nesting birds. Likewise, bird communities have changed due to anthropogenic changes on the landscape. Knopf (1986) found that virtually 90% of the 82 breeding bird species in the shortgrass region of eastern Colorado were not present in 1900. Introduced fish species are also a widely recognized threat to ecosystem integrity; however, in the case of fish much of the movement was a deliberate effort to alter an ecosystem.

Altered Animal Abundance:

Missing Species: The complex and profound effects of species missing from an ecosystem were illustrated in previous models. The absence of species is both an effect and cause of ecosystem disruption and degradation. The absence of species with disproportionately high effects on ecosystems, such as bison, wolves, and prairie dogs, can have especially profound ramifications on ecosystem processes. The absence of large predators, in combination with other stressors, has led to overabundance of ungulates such as deer, elk, and bison in several parks. Every park in the Network suffers from this stressor.

The absence of both fire and grazing can have severe consequences for grasslands. However, whereas fire is absent from many areas, the estimated tens of millions of bison on the Western Plains were replaced by an estimated 45 million cows and an equal number of domestic sheep in 1890 (Fedkiw 1989). Although cattle can replicate some elements of bison grazing, they differ in many other respects. For example, cattle tend to spend more time in riparian areas whereas bison range more widely over the landscape. Perhaps more significantly than the substitution of cattle for bison per se, is that management of cattle for maximum sustained yield of meat production has created a homogeneous landscape by removing the grazing variability historically created by bison. For example, the uniformity of grazing management on the Great Plains probably has a more negative effect on endemic avian assemblages than the actual presence of cattle (Knopf 1996). Current grazing levels and practices are known as “managing for the middle” because they almost uniformly result in a middle seral stage at the cost of early and late stages.

Conceptual Diagrams for Four NGPN Parks

Most NGPN conceptual models focus on a subset of resources important in any park, and are designed for internal use by NGPN staff. Most models were designed by NGPN I&M core staff or adopted from other I&M Networks without extensive discussions with NGPN park managers, because the primary use of the models is by I&M core staff evaluating potential Vital Signs, measures, objectives, and analytical questions. In contrast, NGPN conceptual diagrams were created for use by multiple sub-groups in the NGPN: I&M staff, park interpreters, park resource managers, the public, and other groups. The diagrams use visual imagery and symbols to effectively summarize information about park resources and stressors, facilitating communication among and between technical and lay audiences (Dennison et al. 2007). Compared to other NGPN conceptual models, these diagrams were designed to provide a park-wide summary of important resources and major stressors within individual parks, and were created based on close collaboration between NGPN staff and staff of the University of Maryland Center for Environmental Science (UMCES).

In 2008, UMCES staff led the development of conceptual diagrams for four NGPN parks: Badlands NP, Fort Union Trading Post NHS, Jewel Cave NM, and the Niobrara NSR worked with Network and park staff through a series of meetings and workshops to develop a list of the primary ecological drivers, processes, and threats relevant to each of the four parks. Through iterative discussions with NGPN staff, UMCES developed these four visual ecological conceptual diagrams, illustrating many of the processes and pressures facing these parks today (Figures B-7:B-10).

These initial diagrams focus on four NGPN parks, but capture resources and stressors relevant throughout the NGPN. We discuss this broad-scale relevance for each diagram below.

Badlands National Park: where paleontology, geology, biodiversity, and culture coexist

The rugged scenic beauty of the Badlands National Park owes its origins to highly erodible, fossil-laden sedimentary rocks that form the distinctive pinnacles, gullies, and spires. Between the outcrops,

mixed grass prairie supports many animals including bison, prairie dogs, and black footed ferrets. Threats to the park include illegal fossiling and the invasion of weeds and non-native grasses.

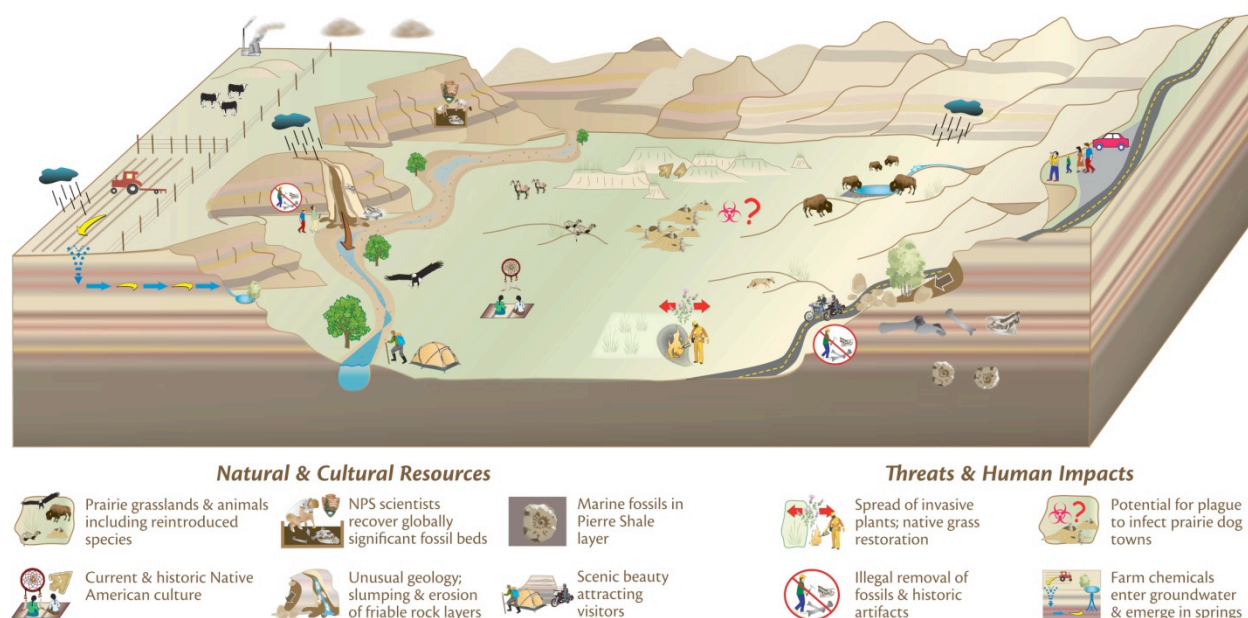


Figure B-7. Conceptual diagram for Badlands National Park.

As at Badlands NP, management of extensive natural areas prized by visitors, large grazers, prairie dogs, and associated fauna are important issues at Theodore Roosevelt NP and Wind Cave NP; prairie dogs are also a management issue at Devils Tower NM and Scotts Bluff NM. Concerns about invasive plants, aquatic pollution from surrounding land uses, and visitor use are high at all NGPN parks.

Fort Union Trading Post National Historic Site: fur trade history brought to life

Nestled along the banks of the Missouri River, Fort Union provides visitors a chance to experience life at an early 1800s fur trading post, prairie grasslands, and river-side habitat. Human impacts to this national historic site include loss of native grass species,

invasive plants, and reduced river flow which is significantly altering riverbank flora and fauna. Efforts to restore and protect the site include planting of native grass species and prescribed fire to control invasive weeds.



Figure B-8. Conceptual diagram for Fort Union Trading Post National Historic Site.

The Fort Union Trading Post NHS diagram re-emphasizes the importance of mixed-grass prairies and scenic vistas prized by visitors, and the threats caused by non-native species and alteration of natural fire regimes. As at Missouri NRR, Knife R. Indian Villages NHS, and several other NGPN parks, aquatic and riparian systems adjacent to Fort Union Trading Post NHS have been drastically changed by dams on the Missouri River. Like many of the NGPN parks, Fort Union Trading Post NHS is far too small to support a full complement of native species, particularly because it is in a heavily fragmented landscape.

Jewel Cave National Monument: pristine cave formations with miles of unique habitat yet unexplored

Jewel Cave, the second longest cave in the world, attracts many visitors who come to explore the calcite crystal-lined passageways. While the cave is largely in pristine condition, there are a number of potential threats that have to be carefully assessed, managed, and

monitored. These include pollution of groundwater that seeps into the cave at various locations and the visitor impacts of changing ambient conditions and the introduction of foreign materials.

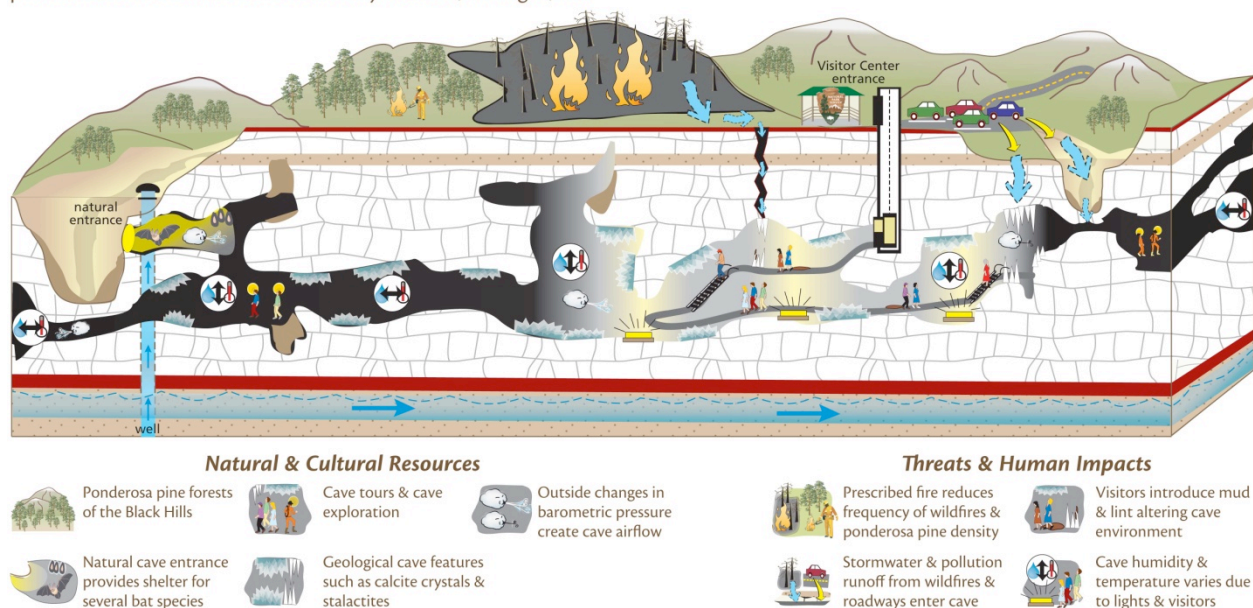


Figure B-9. Conceptual diagram for Jewel Cave National Monument.

The major above-ground issue captured in this diagram is equally important at all four NGPN parks in the Black Hills: management of ponderosa pine forests in the face of altered fire regimes, and the use of prescribed fire to reduce unnaturally high tree densities or tree invasion into grasslands. Many of the resources and issues relevant to Jewel Cave are equally relevant at the NGPN's other globally important cave, Wind Cave. At both caves, geological features and stable interior temperature and humidity levels are key resources parks must protect. Critical stressors at both caves include visitor effects on cave resources and inputs of aquatic pollutants from above-ground sources.

Niobrara National Scenic River: a wild and untamed prairie river with recreational opportunities

The Niobrara is a scenic river where six major biomes converge to form a rich diversity of flora and fauna. The unique geological formations in the park lead to spring-fed streams that flow from the valley walls. Threats to the scenic river arise from fire exclusion

leading to the expansion of ponderosa pine into grassland areas, changes in microclimates leading to loss of northern boreal tree species, spread of invasive plants, and the high volume of visitors during peak periods.



Figure B-10. Conceptual diagram for Niobrara NSR.

The conceptual diagram for Niobrara NSR emphasizes the links between adjacent upland areas and aquatic resources of the river valley. In particular, adjacent land uses, pollutant and nutrient inputs, and water withdrawals are major stressors of the Niobrara NSR. These landscape and aquatic stressors are primary concerns to many NGPN parks.

Terrestrial Ecosystem Models: General Grassland Models

General Ecosystem Model for NGPN Grasslands

Note: The following narrative is adapted from the Southern Plains Network's conceptual model narratives (NPS 2005*b*); it relies heavily on their model description but has been modified to be more relevant to the NGPN.

The North American prairie is a dynamic ecosystem. Dramatic and rapid changes can occur as the result of extreme dry or wet periods, severe winters, summer hailstorms, tornados, thunderstorms, fire, and heavy short-duration grazing by bison and locusts. In modern times some of these disturbances have been attenuated or eliminated (e.g., locusts, fire, short intensive bison grazing); however, new disturbances have occurred (e.g., infestations by exotic plants, cultivation). The extent that the ecological drivers in the region can affect plant communities is well documented in the classic works by Weaver (1943), Albertson and Weaver (1945, 1946), and Albertson et al. (1957) following the Dust Bowl of the 1930s. These studies and others have clearly shown that a particular site can transition from being dominated by tall warm-season grasses to mid-height cool-season grasses to short warm-season grasses and even to woody vegetation.

Temporal precipitation (specifically dry cycles), fire, ungulate grazing and prairie dogs are principle natural major influences on Northern Great Plains grassland ecosystems (Figure B-11). Grazing and fire have generally operated at landscape and local scales, with drought at a broader scale (Fuhlendorf and Engle 2001). Precipitation, evapotranspiration, temperature, and fire all combine to define the boundary where tree growth is possible. Climate and fire are thought to be most important processes to the spread and maintenance of grasslands (Anderson 1990). Where present, prairie dog colonies assert significant influence on prairie grasslands by altering plant species diversity and creating habitats for multiple species of fauna that require close association with the prairie dog species for many of their life requirements. The colonies also have the ability to change the configuration and temporal nature of natural fire regimes, ungulate grazing intensity and distribution, and relationships between soil texture, fertility and moisture over the long term. Below, each of these major influences is discussed. The feedback mechanisms and interactions between weather, soil, fire, grazing, and (in much of the mixed-grass prairie) black-tailed prairie dog, are strong and complex (Figure B-12).

Precipitation Patterns and Variability: As discussed relative to the NGPN general ecological model (Figure B-1), the Great Plains climate is typified by highly variable and stormy weather patterns and increasing precipitation from west to east across the plains (Parton et al. 1981; Risser et al. 1981). Climatic extremes like longer term dry cycles have affected animal and plant abundances for centuries. Bison have died by the thousands in sustained droughts (Roe 1951) and periods of heavy snow and sub-zero temperatures during winter can kill pronghorn. Periodic lack of adequate moisture can affect some grazing during the year of moisture shortage, while

having a lag effect of a year or more on fauna that feed on seeds like small mammals (French et al. 1976).

Temperatures in the Northern Great Plains generally increase from north to south. In the northern most area of the NGPN, average daily temperature in January ranges from -5 to 0 F at Theodore Roosevelt National Park, North Dakota to 5 to 10 F at Scotts Bluff National Monument, Nebraska. Average July temperatures range from 84 to 88 F at THRO to 88 to 92 F at SCBL (HPRCC 1948-2006). Unlike in the Southern Plains, this moderate change in temperature gradient does not result in a significant north-south gradation between cool-season and warm-season grasses. Cool season grasses are most efficient photosynthesizing in cooler temperatures and dominate in the northern or higher elevation plains, where warm-season grasses are more efficient under warmer temperatures (Black 1971), and are more dominant in the grasslands that make up the far southern end of the Network such as in the Nebraska Sandhills. The majority of the NGPN prairie grasslands are characterized by a diverse mix of cool and warm season grasses and forbs (Küchler 1964).

In addition to seasonal variation, Great Plains weather patterns are also highly variable from year to year and decade to decade. The inherent unpredictability of precipitation across years had influence on the evolutionary processes of the Great Plains (Mock 1991). Drought can lead to massive local extinctions of annual forbs and grasses that have invaded stands of perennial species, and re-colonization can be slow (Tilman and El Haddi 1992). The Great Plains, short-grass prairie and particularly the mixed-grass grasslands that make up much of the NGPN landscape undergo frequent long term periods of reduced precipitation, increased evapotranspiration, and increased water runoff (Weaver, 1968; Wilhite and Hoffman 1979). Multi-year dry cycles have ranged from 10-20 years over the past few centuries are a regular events. Organisms that live in this area must be adapted to surviving these periods of drought and increased stress. Significant reductions in normal moisture regimes can have significant affects on plant communities, reducing vegetative cover, changing species composition, lowering flowering rates, and increasing wilting conditions. These dry periods are actually “normal” events and many of the more common plants, such as sideoats grama (*Bouteloua curtipendula*), blue grama, (*Bouteloua gracilis*) buffalo grass, (*Bouteloua dactyloides*) and western wheat grass (*Pascopyrun smithii*), in the NGPN are better adapted to persisting in dry periods and in some cases take advantage of drought conditions (Weaver 1954).

Fire: Fire frequency and seasonality play a large role in the ecology of the Great Plains. Frequent fire is essential to maintain native species diversity, and it affects other components, including nutrient cycling and productivity (Collins and Wallace 1990). Historically, lightning and Native Americans were the principal instigators of fire. In the NGPN, fires ignited by summer storms occur May through September (70+% of them between late June through early September) when storms are most common (Bryson and Hare 1974). Native Americans appeared to use fire most frequently in July and August (Moore 1972). Lewis and Clark found the mixed-grass prairie “much parched with frequent fires” (Lewis 1961:66). In shortgrass communities, fires were less frequent, although they were reported by early travelers and were still a major

influence (Brockway et al. 2002). Large mammals, such as pronghorn, elk, and bison, concentrated on burned areas (Lewis 1973; Evans and Probasco 1977) and burning was used by Native Americans for hunting (Moore 1972).

Climate and fire have been the biggest factors in determining if grasslands preclude forests in the Great Plains region (Axelrod 1985; Anderson 1990). Fire can interact within extreme dry periods by affecting the amount of fuel available, the influence of precipitation on prairie post-burn, and the moisture content of the vegetation can determine where fires are possible (Anderson 1990). The interaction of fire with grazing has a profound effect on the composition, structure, and processes of Great Plains plant communities. Fire-induced mortality of woody plants is tied to their morphology and life-history traits (timing of above ground growth, translocation of carbohydrate reserves, unprotected aboveground meristems). Grasses can die down so that only underground portions are maintained with dead tops above the surface. This adaptation helps them survive fire as well as dry periods. Growing points beneath the surface allow the plants to re-grow after fire and grazing have removed the above ground tissues. Productivity of grasslands is generally enhanced by the removal of excess biomass (standing and dead litter) through grazing or periodic fires (McNaughton 1979; Risser et al. 1981; Anderson 1982; Dyer et al. 1982; Knapp and Seastedt 1986).

Fires can burn extensive areas in the Great Plains due to the combination of flat and rolling terrain with winds from the south and west. Natural fire breaks would have existed outside the Black Hills, along streams in the form of gallery forests (Abrams 1986), in areas that recently had been heavily grazed by bison or sites inhabited by prairie dogs. Pre-European fires were likely much larger than the prescribed fires and wild fires that occur today. Historical accounts of nineteenth century immigrants identify the significance of frequent, large fires (Mattes 1969).

Today, increased livestock grazing keeps fuel loads lower which, in turn, reduces fire intensity across the Great Plains and eliminates it almost entirely in portions of the short-grass prairie. Prescribed fires are small, controlled, and generally conducted on days when the fire is most easily contained. Some NGPN parks have not had prescribed fire for decades, some are recently considering prescribed fire and developing fire management plans and others, such as Devils Tower NM have used prescribed fires extensively over the past two decades.

Ungulate Grazing: In the Great Plains, bison were the dominant grazer during pre-European times. Bison preferentially target grasses vs. other plants (Peden et al. 1974; Meagher 1978; Schwartz and Ellis 1981; Plumb and Dodd 1993; Steuter et al. 1995). In 1845, Fremont wrote that bison ‘scarcely left a blade of grass standing’ (White and Lewis 1967:320). Therefore, bison grazing alters the competitive relationship among plants and results in a heterogeneous landscape with distinct grazed patches (Fahnestock and Knapp 1993, 1994; Catchpole 1996). Bison grazing can alter spatial heterogeneity and relative abundance of certain plant species (Coppedge et al. 1998; Knapp et al. 1999).

Bison and other ungulates can increase aboveground productivity (Frank and McNaughton 1993) and can dramatically alter nutrient cycling (Day and Detling 1990; Frank et al. 1994; Frank and Evans 1997; Knapp et al. 1999). Grazing can stimulate nutrient uptake and increase soil nitrogen concentrations (Coppock et al. 1983; Jaramillo and Detling 1988; Green and Detling 2000). In addition ungulates can increase rates of de-nitrification (Groffman et al 1993), ammonia volatilization (Schimel et al. 1986; Frank and Zhang 1997), net nitrogen mineralization (Holland and Detling 1990) and nutrient redistribution through urine and fecal deposition (Day and Detling 1990; Frank and Evans 1997).

Grasslands in the Great Plains have evolved with grazing. Nodal rooting, or underground branching, thorns and spikes, secondary compounds that are difficult to digest, and general unpalatability are evolutionary responses of the long co-evolutionary association between plants and grazing animals. Below ground processes have also evolved with grazing. Soil dwelling herbivores and detritivores often increase under moderate grazing, but decline under heavy grazing (Seastedt et al. 1988). On a much smaller scale, the plains pocket gopher (*Geomys bursarius*) is an important vertebrate due to its burrowing and mounding activities which alter essential plant resources similar to the effects of prairie dog colonies. Root herbivory occurs underground and the deposition of subsurface soil in mounds above ground buries plants and alters light, water, and nutrients. Mounds are strongly clumped in a uniform pattern which influences the adjacent plant community. Plant growth is inhibited over the disturbance, and an increase in resources and plant growth adjacent to the disturbance results in a competition-induced wave of biomass emanating out at least 20 inches (50 cm) from the disturbed site

However, different levels of grazing can have dramatically different effects. Under certain conditions, grazing can increase species diversity (Bakker and Ruyter 1981). In the short-grass prairie, moderate levels of grazing can stimulate growth of dominant grasses with rapid growth that helps them to maintain a competitive edge over invading grasses and forbs (Risser 1990). Heavy grazing can change the plant community and can lead to losses of pollinators and seed dispersers and fossorial animals that aerate the soil and are involved in nutrient cycling (Stafford Smith and Morton 1990; Yeaton and Esler 1990). Overgrazing can increase water runoff and erosion by reducing infiltration of water (Fuls 1992; Thurow et al. 1988) in part due to a reduction in soil-dwelling insects that aerate the soils (Whitford 1986). This reduction in water conservation leads to reduced grassland productivity and in extreme cases can contribute to desertification of these landscapes (Schlesinger et al. 1990).

Grazing has direct and indirect effects at landscape and regional scales, which, in turn, interact with other small-scale and large-scale factors to heighten temporal and spatial diversity in grasslands (Gibson and Hulbert 1987; Risser 1990). Grazing and low precipitation can combine to affect heterogeneity in plant composition. For example, blue grama and buffalo grass are dominant grasses in shortgrass prairies or in heavily grazed areas of mixed-grass systems. Both are similar in phenology and can withstand heavy grazing. Blue grama is thought to be able to better withstand dry periods (Albertson and Tomanek 1965), but buffalo grass increases in

abundance under heavy grazing (Savage and Jacobson 1935) and has higher photosynthetic rates at low temperatures (Monson et al. 1983).

Historically fire and grazing interacted through a series of positive and negative feedbacks that resulted in a shifting mosaic of vegetation patterns across the landscape (Hobbs et al. 1991; Fuhlendorf and Engle 2001, 2004). The probability of fire is greatest on areas with high biomass accumulation within a grazed landscape, a result of low grazing pressure. Grazing animals in turn are attracted to the most recently burned areas (Coppedge et al. 1998; Coppedge and Shaw 1998). Through grazing, biomass is reduced, more bare ground is present, and the probability of fire is reduced. Lack of fire leads to reduced grazing, the grass then recovers and becomes more susceptible to burning. This patchy landscape had a profound effect on other vertebrate fauna. For example, grassland birds occupy a wide range of grasslands from heavily grazed to ungrazed (Knopf 1996). Grazing is not limited to ungulates, as black-tailed prairie dogs can have a modifying effect, particularly in short-grass systems. A positive feedback between prairie dogs and other grazers results in increased use of these areas by bison and pronghorn (Coppock et al. 1983; Coppock and Detling 1986; Kreuger 1986).

Grazing is still a dominant process in the Great Plains, but the timing, intensity, species, and duration have all changed substantially. Modern range practices with livestock generally do not produce the landscape heterogeneity produced by historic grazing patterns (Hart and Hart 1997). Grazing practices are focused on uniform disturbance through uniform distribution of grazing animals on temporal and spatial scales. Bison grazing would have been high intensity, low frequency grazing that would have given most species a chance to recover during long rest periods. In some parts of the Great Plains, overgrazing can produce a shift from grasses to plant assemblages dominated by woody plants (Westoby et al. 1989) and may encourage invasion of non-native exotic species such as saltcedar (*Tamarix* spp.) (Schwartz et al. 1996). Cattle also tend to congregate in riparian areas more than bison, which can lead to degradation of the entire ecosystem (Martin and Ward 1970; Foran and Bastin 1984; Fuls 1992; Watkinson and Ormerod 2001; Landsberg et al. 2003; Tobler et al. 2003).

Discrete fires and patch selective grazing can cause shifting mosaic across the landscape. NPS park units need to be aware of the land management on surrounding areas when determining their place in a heterogeneous landscape. Grazing has primarily been accomplished through fencing which enables management agencies to establish standardized guidelines for removal of grazers from ecosystems. As fencing increases, the heterogeneity decreases and the probability for a suite of viable species, such as grassland birds, decreases. Standard management practices preclude endemic species that exist at the ends of the grazing gradients (Knopf 1994).

Black-tailed Prairie Dogs: Although currently occurring at only five NGPN parks, historically black-tailed prairie dogs were widespread across the region, and likely occurred in or near most parks except for Jewel Cave NM and Mount Rushmore NMEM. In mixed-grass ecosystems of this region, prairie dogs join fire, precipitation, and ungulate grazing as a major factor

influencing grassland communities. Prairie dogs are also a dominant grazer but are much less mobile and spatially influential than bison. Prairie dogs can affect the graminoid biomass and ratio of grasses to forbs (Cid et al. 1991), reduce biomass of roots while increasing density of nematodes (Polley and Detling 1988, 1990; Whicker and Detling 1988). Grazed plants in prairie dog towns have higher nutritive value than uncolonized grassland (Kaufmann and Kaufmann 1997), which subsequently leads to increased grazing in prairie dog towns by large herbivores. Uresk and Paulson (1988) estimated that 300 prairie dogs consume about the same amount of vegetation as a cow calf pair.

Prairie dogs have additional roles in grassland systems besides acting as grazers. The presence of a colony increases the chances that other rare species such as mountain plovers (*Charadrius montanus*) (Knowles et al. 1982; Knopf 1996), ferruginous hawks (*Buteo regalis*) (Cook et al. 2003), burrowing owls (*Athene cunicularia*) (Desmond et al. 1995) and swift foxes (*Vulpes velox*) (Agnew et al. 1986) will be present. Their tunnel system also provides refuge; albeit habitats for a variety of taxa ranging from invertebrates to amphibians and reptiles. The prairie dogs also play an important role in nutrient and soil cycling and as prey species for higher trophic levels.

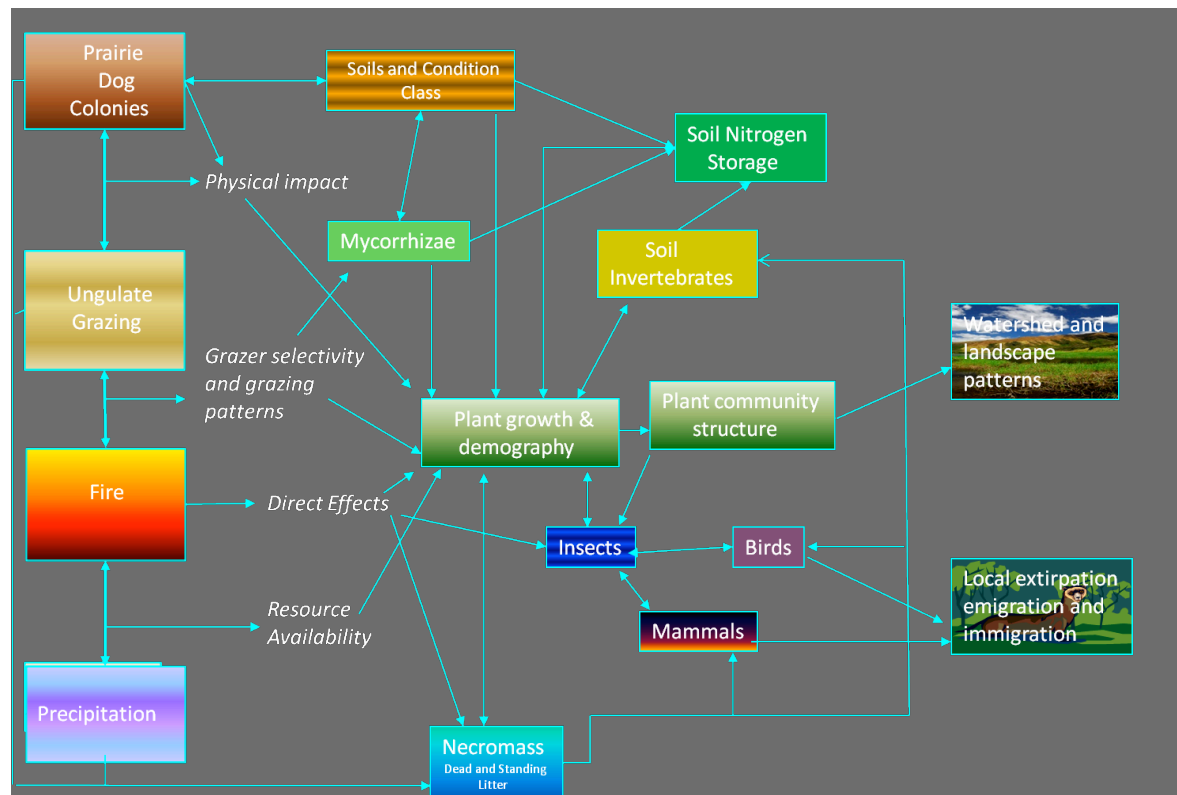


Figure B-11. General model of Northern Great Plains mixed-grass prairie ecosystems. The model shows core abiotic and biotic relationships within terrestrial grassland ecosystems in NGPN parks. Modified from L. Thomas's (NPS) unpublished adaptation of model from Hartnett and Fay (1998).

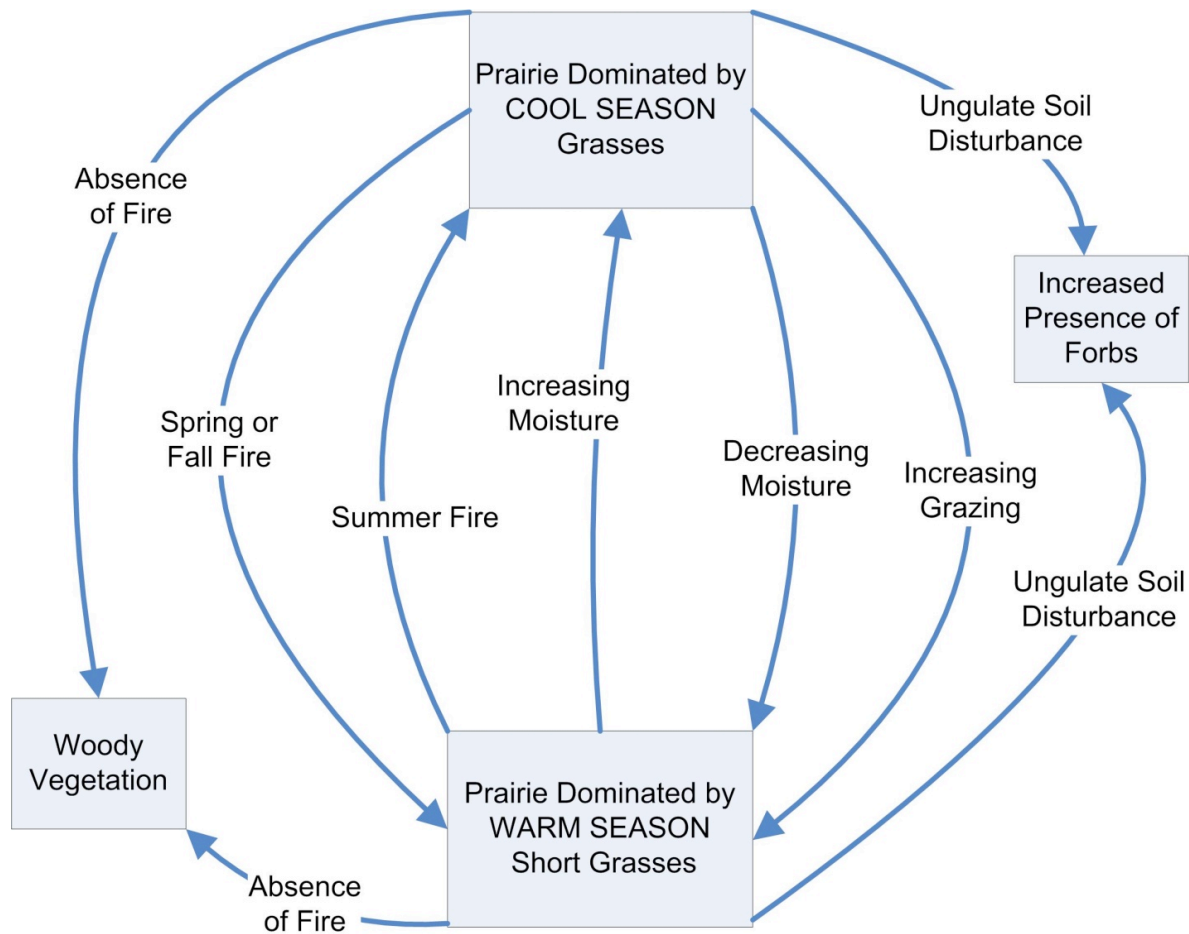


Figure B-12. General response of grasslands to fire, grazing, and precipitation. For purposes of simplicity and comprehension the model applies only to the Northwestern Great Plains region as delineated by Omernik (1987), i.e., it does not apply to the more eastern tallgrass region and the Sandhills region of Nebraska. The purpose of the model is to show how the ecological drivers in the region change plant communities spatially and temporally.

Nutrient Dynamics

As a general statement, nutrient availability in the Northern Great Plains tends to be low compared to other ecosystems, with the lowest concentrations in the more western part of the region. This is primarily due to the hot dry climate. However, nutrient availability varies both spatially and temporally due to the variable weather (primarily precipitation and temperature) and the dynamic nature of the other ecological drivers in the system such as fire and short duration intensive grazing (Figure B-13). Nutrient pathways mediated by herbivores and fire are rapid whereas other pathways (e.g., litterfall) are slower. Yet there are exceptions to the pattern. For example, chronic heavy grazing and trampling can stress plants and slow and reduce nutrient transport within plants.

Grazing and fire patterns across the landscape create a heterogeneous landscape of varying nutrient levels and transport rates, which result in differing feedbacks and controls, further adding diversity to the system. The amount of soil nutrients can directly influence plant composition and abundance at a site. Under some conditions nitrogen and carbon levels can be surprisingly high due to the complex feedback mechanisms between fire, grazing, and plants. Seastedt (1995) concluded that the current accumulation of nutrients in prairie soils can best be explained by a history of infrequent grazing and infrequent fires.

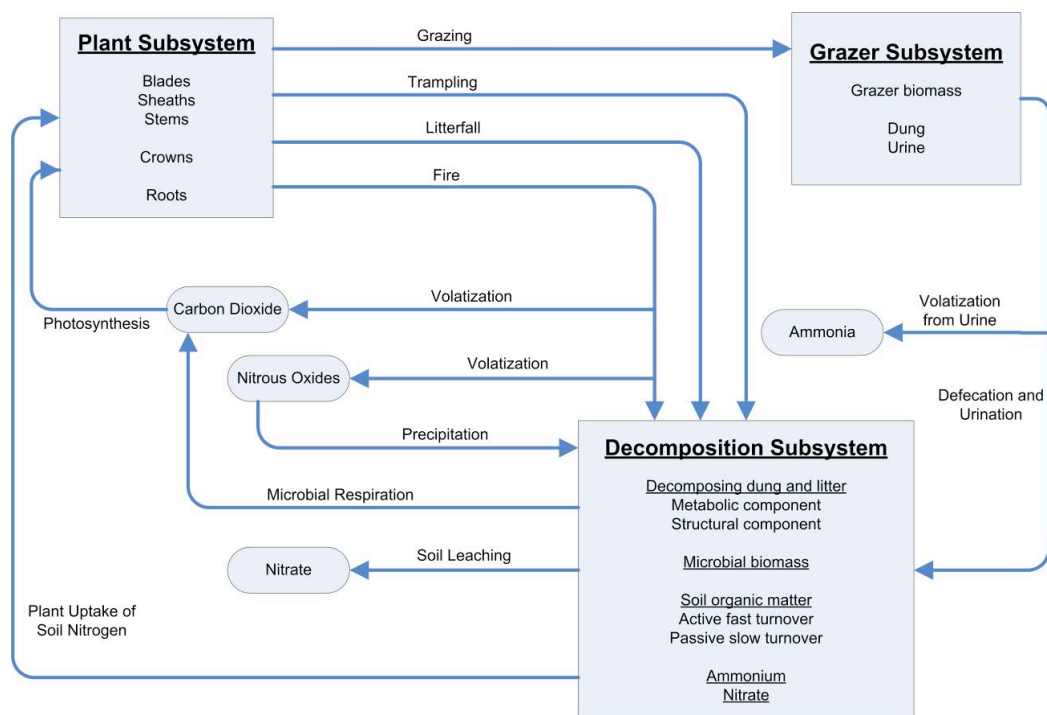


Figure B-13. Nutrient cycling in grasslands of the Northern Great Plains. Revised from McNaughton et al. (1988).

State-Transition Models for NGPN Vegetation

Introduction

To summarize major vegetation types and processes affecting these types in the NGPN, we developed state-transition models (e.g., Briske et al. 2005) for selected NGPN vegetation communities. We developed state-transition models for several reasons. First, by deciding which site types to model, we improved our understanding of the range of vegetation types found in the NGPN and the factors (e.g., soil type) that distinguish these types. Second, creating models and defining transitions among states increased our understanding of how important drivers, interactive factors, and stressors produce transitions among grassland types. In particular, we focused on effects of soil type and topography, grazing and browsing, fire, and precipitation. Third, the models form a framework for describing the ecological conditions of the NGPN in greater detail. Collectively, the models summarize the range of vegetation communities, habitat types, and successional states across the central and western NGPN.

We used Ecological Site Descriptions and state-transition models from NRCS, models from other sources, discussions with area ecologists, and professional judgments to form state-transition models for major vegetative types in the NGPN. Our models focus on major habitat types at NGPN units where plant community composition will be monitored. Additional models for relevant plant communities at Niobrara NSR and Missouri NRR may be developed for types targeted by NGPN monitoring. We used USGS-NPS Vegetation Mapping Program reports (Salas and Pucherelli 1998*a*, 1998*b*, 1998*c*, 2003*a*, 2003*b*; USGS undated *a*, *b*, *c*, *d*; Von Loh et al. 1999, 2000) for most NGPN parks (Niobrara River and Missouri River reports were not available), other literature, and discussions with range ecologists to determine major vegetation types for this modeling.

These models are an attempt to capture our understanding of major vegetative states and conditions that have occurred in recent decades in Network parks. These models, like any model, are simplified descriptions of complex systems. Some of the simplifications made by these models include the following:

- The models qualitatively define discrete site types and vegetative states. In reality, sites do not fit cleanly into the types and states within types described by our models. Instead, there is continuous gradation among these categories; sites often share characteristics of multiple states.
- These models are unlikely to capture the full range of variability we can expect over the next century. Current species associations that define states may be temporary over multiple centuries, and species that currently co-dominate a state may move independently in response to climate change or other environmental trends. Vegetative conditions observed in the recent past may have formed in response to conditions and events hundreds of years ago (e.g., a favorable period for pine establishment in the Black Hill [Brown 2006]; more speculatively the

effects of tree clearing on floodplains adjacent to forts and steamboat landings in the 1800's). In the shorter term, species respond individualistically to disturbances such as fire or grazing (e.g., West and Yorks 2002).

- These models show one or more deterministic pathways following disturbance of any state, under the assumption that a site's pathway can be predicted by the site environmental and soil characteristics, the site conditions at the time of disturbance, and the disturbance characteristics. However, the pathway followed by any site will still have a random element superimposed on these other factors – for example, from the interplay of random dispersal/colonization processes and the vegetation characteristics of the area surrounding a disturbed patch (Hubble 2001; Gravel et al. 2006).
- Even under a stable climate, the range of states possible for a site likely is much broader than we hypothesize. The history of grasslands classification at Conata Basin adjacent to Badlands NP illustrates how seemingly permanent community classifications can easily be inaccurate. Küchler (1964) considered this basin to be in a pocket of short-grass prairie because it was dominated by blue grama and buffalograss. However, this shortgrass-dominated state was a result of ~100 yrs of livestock grazing. When grazing was reduced and prairie dogs poisoned during the late 1970's to early 1980's, mid-height grasses (western wheatgrass and needlegrasses) became dominant (D. Uresk, USFS, pers. comm.), and are the natural dominants of late-seral stages at Conata Basin (Uresk 1990). Description of the NGPN region as short-grass prairie (Bailey 1995; Primm et al. 2001) reflects effects of domestic grazing rather than the potential vegetation (mid-height and mixed-height grasses) under low grazing regimes (Lauenroth and Milchunas 1992:185).

However, such limitations do not make these models useless. In contrast, we cannot understand potential threats to our ecosystems without understanding the current range of variation in community dynamics. These models are a framework for discussing potential impacts of climate change, invasive species, nitrogen fertilization, and changes in hydrology. Our models represent the current knowledge of the NGPN I&M staff in terms about relevant vegetation types and states within each type, and the general effects of disturbance on these types. Inherent in each model is an underlying hypothesis about the range of potential states possible for each type during the next few decades. The models should be refined as we discuss them with park staff and other experts in each area.

This need for refinement is especially critical in the context of invasive species and climate change. By necessity, these models largely portray the recent past: conditions and processes documented over the last century (along with a multi-century perspective of fire histories in the Black Hills). The NGPN systems now contain numerous invasive species and are likely to face rapid changes in temperature and precipitation amount and timing. Currently, our models incorporate invasive species and climate fluctuations only generally. A next step in making these

models useful is to examine in more detail how climate change and invasive species may alter the fundamental conditions of a site and the vegetative states likely to form after disturbance. This effort could help us to identify early warnings of major impending changes that are not in the range of transitions documented over the last several decades

Northern Mixed-grass Prairie: Grassland Types

“Classification of vegetation is difficult because of the great heterogeneity due to variations in topography, soil conditions, wind and water erosion, water penetration, and to the various kinds of succession and stages in succession. Seres are occurring on recently eroded banks, on recent depositions, on saline depressions, on sandy hills and ridges, on abandoned cultivated lands, on an areas depleted by grasshoppers, drought, and overgrazing. (Hanson and Whitman 1938:108)

Grassland models followed the format of NRCS Ecological Site Description state-transition models for NRCS Major Land Resource Area (MLRA) 60A (Pierre Shale and Badlands) in southwest South Dakota, and MLRA 64 (Mixed Sandy and Silty Tableland) in southwest South Dakota and northwest Nebraska (NRCS 2007). We used these models as guides, but could not copy these models completely. The available NRCS models did not directly cover most NGPN grasslands, except for those in Nebraska parks and portions of Badlands NP. Although we followed the general NRCS-modeled transitions caused by fire, grazing, and precipitation, some states and transitions relevant to NPGN parks were different than those in the NRCS models. In addition, separate NRCS models are created for each of a large number of site type (e.g., several different categories of loamy soils). We defined site types that pooled numerous NRCS types that shared common transitions and states (e.g., condensing into one model all models characterized by dominance of western wheatgrass under pre-settlement grazing and fire regimes).

We defined four vegetation types to cover upland grasslands in NGPN parks: a) the western wheatgrass/green needlegrass/needleandthread type most frequently present on loamy and clay soils; b) the needleandthread/threadleaf sedge/blue grama type found on upland coarse soils, particularly on ridges and upper slopes; c) little bluestem or big bluestem types found on shallow loamy and rocky soils; and d) sandy types characterized by prairie sandreed, needleandthread, sand bluestem, and sand sagebrush.

Our models treat these four types as distinct from one another. However, most park grasslands will be a heterogeneous mix of types, with patches of each type ranging in size from several thousand to <100 m². Usually, the borders between types will be indistinct and possibly dynamic, particularly because most of the grasses characterizing states in one type can also be dominant in other types. Moreover, shrublands and woodlands are interspersed, creating landscapes that are spatially and temporally heterogeneous at numerous scales. Grasslands of NGPN parks grasslands characterized by high heterogeneity, particularly in complex topography such as the White River badlands in western South Dakota and the Little Missouri badlands in western North Dakota.

Our current models do not adequately cover several grassland types or states. At Knife River IV NHS, big bluestem dominates some moist meadows; transitions in this tallgrass-prairie type likely are different than in the big bluestem type of slopes at Wind Cave NP. A model covering big bluestem meadows would also be relevant in areas of the Niobrara NSR (Kantak 1995) and Missouri NRR. Some sites in the Nebraska Sandhills south of the Niobrara NSR may be covered by our sandy-site model, but additional models would be needed to cover the range of Sandhills types. Current models do not cover restoration sites (e.g., at Fort Union Trading Post NHS) and those dominated by *Bromus* or crested wheatgrass at numerous parks.

In all of the grassland models, a transition to a woody-dominated state is modeled as unlikely or not possible on most sites, even in the absence of fire. Woody encroachment into grasslands is a major conservation problem in much of the Great Plains, including central and eastern Dakotas and Nebraska (e.g., Grant et al. 2004). However, away from the Black Hills and other high ridges, low moisture availability restricts shrublands and woodlands to more mesic topographic positions and soil types (Girard et al. 1989). In the NGPN encroachment is a problem primarily with pine in the Black Hills foothills, and with pine and *Juniperus* in limited portions of Scotts Bluff NM and the Nebraska Sandhills. These areas are covered in the foothills/savanna model. In addition, encroachment by eastern red-cedar is a bigger problem in the area of Niobrara NSR (Figure B-10) and Missouri NRR; these parks are not explicitly covered by the current grassland models, but these situations are partially covered by the foothills/savanna model. Further examination is needed to determine whether increased encroachment or loss of shrubs is more plausible with long-term changes in precipitation amounts over a time scale of several decades. Further discussion is needed to determine if shrub encroachment is significant at Knife River Indian Villages NHS or other NGPN parks.

Western wheatgrass/green needlegrass/needleandthread type (Figure B-14): Western wheatgrass/green needlegrass and wheatgrass/needleandthread grass communities occur extensively on relatively mesic clay and loam soils at Badlands and Theodore Roosevelt National Parks, in grassland portions of Wind Cave NP, and as smaller patches in grasslands of several other parks. This type often is present on flats and lower slopes adjacent to upper slopes and ridges dominated by needleandthread or little bluestem types. This is the most common type across much of the Northern Great Plains (Martin et al. 1998), particularly in western South Dakota.

On most sites, annually reoccurring grazing at moderate levels or prolonged drought leads to a decrease in western wheatgrass and needlegrass and increase in short warm season grasses, particularly blue grama and buffalo grass, as well as threadleaf sedge. If grazing is reduced to intermittent levels with long rest periods between grazing, this stage will succeed back to the later seral stage dominated by cool season mid-grasses. With prolonged or heavy regular annual grazing moving the site to an early seral stage, the cool mid-grass component is reduced, eventually leading to blue grama / buffalo grass dominance (Uresk 1990). Although *Opuntia* is

present throughout this type, it becomes most abundant with heavy grazing on heavier claypan sites.

In this region, transitions from wheatgrass to shortgrass or to prairie dog towns are reversible once grazing is reduced. Under recent precipitation levels (i.e., over the last several decades), most sites in the Northern Great Plains recover without intensive management after cessation of heavy grazing, even after several decades of heavy grazing in some situations. Although this recovery may take >9 yrs (Uresk 1985), it is rapid compared to drier sites in the shortgrass region and southern Great Plains (D. Uresk, USFS, pers. comm.). However, with a long-term shift to a much drier climate, shortgrass species would become more dominant, and a state resulting from heavy grazing would be highly resistant to change.

On mesic portions of the western wheatgrass zone or with prolonged wetter years, absence of fire plus either repeated seasonal grazing or prolonged absence of grazing leads to increased density of the non-native Kentucky bluegrass. In the absence of both fire and grazing on these sites, litter accumulates. Snowberry and other shrubs may increase in height and perhaps cover, although transition to a shrub-dominated state is unlikely. If these conditions are prolonged, native grass cover decreases further and exotic *Bromus* spp. increase. In the absence of fire, with no or heavy grazing, bluegrass may become dominant on mesic sites or with prolonged moist conditions. Throughout grasslands of the NGPN, *Bromus* and other exotic species have established in road cuts (often after seeding) or other disturbed areas. In the absence of fire and grazing, litter buildup has allowed establishment of Japanese brome (*Bromus japonicus*) in patches at Badlands and other NGPN units. Repeated burning or drier condition can reduce cover of this species (Whisenant and Uresk 1990). On mesic sites in the central Dakotas and western North Dakota, smooth brome (*Bromus inermis*) can establish and outcompete native grasses, forming dense stands highly resistant to restoration. At Theodore Roosevelt, smooth brome also has colonized grasslands adjacent to disturbed areas (Von Loh et al. 2000). Whether dominance by native vegetation can be restored on invaded sites is a question of high management concern to NGPN managers. Whether as a dominant or subordinate part of the community, Kentucky bluegrass may be difficult to remove once established. Repeated fires may allow native species to recover dominance over Kentucky bluegrass on ridges and drier sites, but may be less effective in reducing bluegrass dominance in swales (USGS 2006).

Several other transitions are possible for the wheatgrass/needlegrass state depending on soil type, moisture availability, geographic location, and proximity to woody cover types. Big sagebrush communities are minor or absent in most NGPN parks except at Theodore Roosevelt NP, where they occur as in topographic positions that retain higher soil moisture than the surrounding grasslands, or as sparse badlands communities. However, big sagebrush communities occur more regularly in the surrounding landscape of the western part of the region. In eastern Wyoming and Montana where precipitation is higher, transitions to states dominated by big sagebrush are possible (Kudray and Cooper 2005). In the absence of fire and with season-long grazing reoccurring annually, colonization of grasslands next to these stands may occur; shrub density and importance of blue grama increases. Eventually, the site may convert into a sagebrush

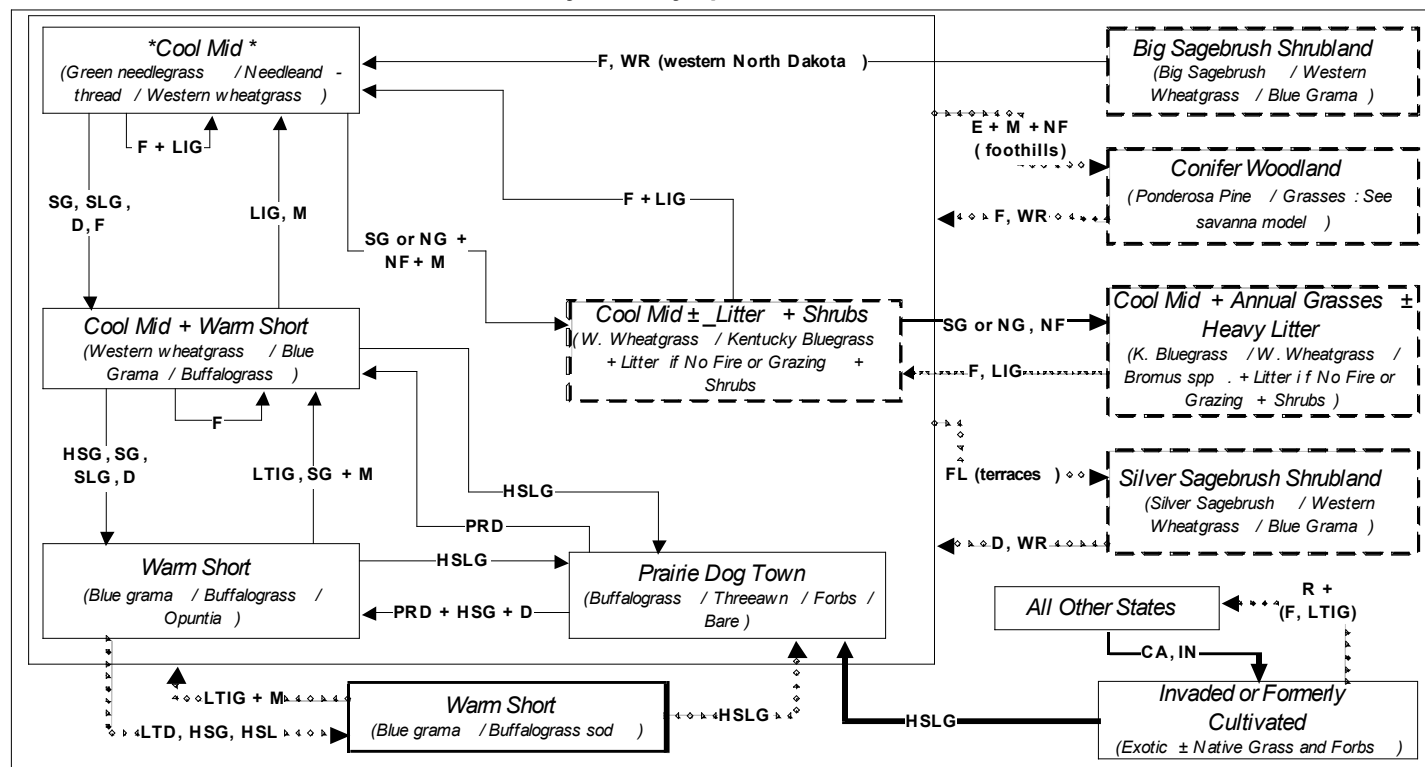
shrubland with cool season mid grasses limited to microsites protected from grazing by the shrubs. However in the NGPN units which are at the edge of the sagebrush zone, encroachment by sagebrush likely is very slow and unlikely under current precipitation levels (D. Uresk, USFS, pers. comm.). The opposite transition, with loss of sagebrush and conversion to a grassland type, is possible for a small number of sites in the NGPN.

Similarly, encroachment by snowberry or other shrubs into adjacent grasslands occurs slowly or only in localized areas even though the western wheatgrass often supports low density of scattered shrubs and many small patches of dense snowberry or other species in moist microtopographic positions. Conversely, snowberry and several other dominant shrubs are stimulated by fire and not removed by grazing, making shrubland-to-grassland transitions unlikely except for sagebrush-dominated sites.

At Wind Cave NP and Devils Tower NM, western wheatgrass communities may be present as openings in pine forests and savannas. In these areas, prolonged fire suppression can allow conifer seedlings to get established in the adjacent grasslands, potentially leading to open woodlands or dense stands. However, these transitions are covered in the foothills / savanna model. Throughout NGPN parks away from the Black Hills, we modeled conifer encroachment as a rare transition that is not possible even near existing conifer patches in grassland parks. In these parks, Rocky Mountain juniper and Eastern red-cedar may be present in dense stands in steep draws adjacent to the western wheatgrass type. Juniper and pine woodlands may be present on steep slopes and on ridges and buttes. Away from the Black Hills in the NGPN, ponderosa pine and Rocky Mountain juniper are limited by soil type, and encroachment to adjacent grasslands is rare (D. Uresk, USFS, pers. comm.). Encroachment probably is a risk only on loamy and clay soils types under prolonged mesic conditions. For example, little encroachment has been noted at Badlands and Theodore Roosevelt NPs. Further east in the Northern Great Plains, encroachment by eastern red cedar is widespread. This species or hybrids with Rocky mountain juniper occur at Scotts Bluff and Badlands.

When occupied by prairie dogs, any of the grassland states in this site type become characterized by bare ground, dominance of short grasses such as threeawn and buffalograss, and high relative contribution of forbs. Because of the complexity of dynamics associated with prairie dogs, we developed a separate state-transition model is needed for prairie dog towns. We summarize relevant dynamics briefly here. Colonization by prairie dogs occurs in areas without tall vegetation cover, such as in areas after drought or prolonged grazing. In the Badlands, some towns become dominated by bare ground but most towns maintain cover of buffalograss, even when animal densities and precipitation are similar. At Wind Cave NP, more prairie dog towns may be dominated by bare ground as a result of grazing and recent drought. In the Badlands NP area, rapid transitions from bare ground or shortgrass states back to dominance by western wheatgrass occur in mesic years when prairie dogs are removed (D. Uresk, USFS, pers. comm.).

**Western Wheatgrass / Green Needlegrass / Needleandthread Type
Loamy and Clay Upland Sites**



States	Transition Types	Transition Agents
Possible for most sites	No Threshold Crossed	LIG, LTIG / NG = (Long -term) intermittent grazing with long rest periods / No grazing
Potentially occurring in restricted conditions of moisture , topography , or adjacent states	Transition Across Threshold	SG, HSG: (Heavy) reoccurring seasonal grazing
	Threshold transition requiring long time and high effort or not widely applicable	SL, HSL: (Heavy) reoccurring season -long or continuous grazing
		F/NF: Fire , No fire
		E/WR = Woody encroachment / Removal : brush or logging treatment
		CA: Cultivation or other conversion followed by abandonment
		IN/R: Invasion / Exotic removal
		D/LTD: Prolonged (multi -year) / Long -term (multi -decade) aridity
		M/FL: Prolonged mesic conditions / Site turns into floodplain due to river rise or meander
		PDR: Prairie dog removal or die -off

Figure B-14. State-transition model for NGPN western wheatgrass site types.

Note: NRCS models for many clay site types are simpler than this overall model, often showing only 3 states (wheatgrass/ wheatgrass/shortgrass, and shortgrass states). Based on conversations with D. Uresk, USFS, (USFS, Rapid City) transitions to woody-dominated states (away from the Black Hills) and transitions across a threshold to a shortgrass-dominated state were considered unlikely or not possible for most sites without prolonged climate change.

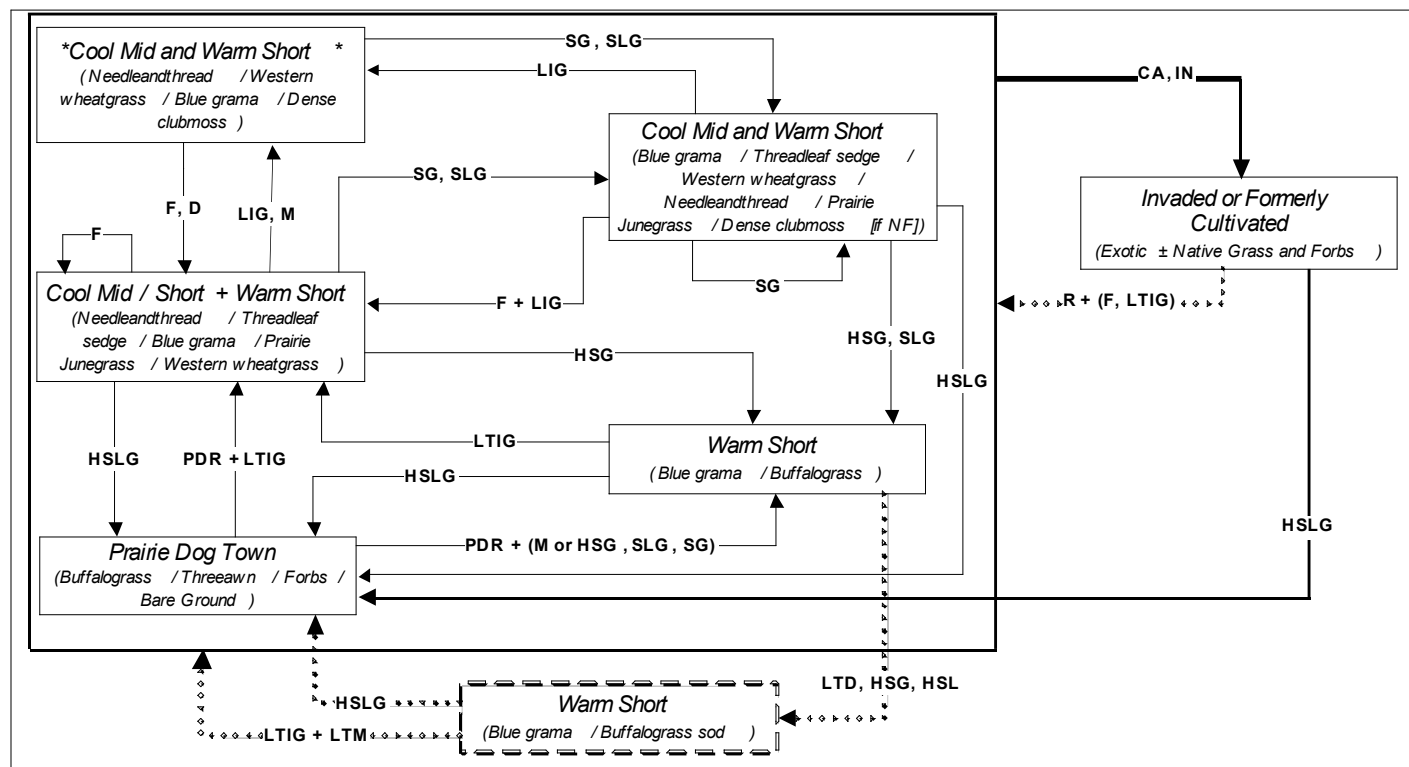
Needleandthread/sedge/blue grama site type (Figure B-15): The needleandthread/threadleaf sedge/blue grama community is an extensive grassland type that is adjacent and often intergrades into the western wheatgrass type. These two types are the most common communities of Northern Great Plains grasslands (Martin et al. 1998). In the NGPN, the needleandthread state is most abundant at Theodore Roosevelt NP where it often occurs on drier upland sites with deep sandy to loamy soils. The western wheatgrass group typically occurs in adjacent areas downslope, where soil moisture is higher (Von Loh et al. 2000). Where these types intergrade, transitions characteristic of either type or a hybrid of the types are possible. The needleandthread type is also widespread at Scotts Bluff and Agate Fossil Beds NMs, and around Fort Laramie NHS.

Under intermittent grazing and frequent fires, these sites have high cover (60-100%) dominated by mid-height grasses, with high frequency but low cover of subshrubs, particularly fringed sage. At Theodore Roosevelt NP, dense clubmoss (a spikemoss, *Selaginella densa*) forms mats at the ground surface, averaging 48% cover in needleandthread stand (Hansen et al. 1984). Dense clubmoss may persist and increase in the absence of fire or with moderate grazing (Van Dyne and Vogel 1967; Hauser 2006). However, dense clubmoss infestations have not been noted as a threat to carrying capacity and plant diversity of this region, in contrast to rangelands of Montana (Ryerson et al. 1970). Dense clubmoss is absent or a minor element in grasslands of NGPN parks in South Dakota and Wyoming.

Several transitions from the “climax” needleandthread state are not well defined, and lie along a grazing- and moisture-driven continuum from greater to lesser amounts of needleandthread vs. western wheatgrass and other species. With regular moderate grazing or prolonged drought, it was assumed that threadleaf sedge, blue grama, and prairie Junegrass (Simonin 2000a) would increase, while needleandthread would decline. With continued heavy grazing, a transition to a warm season shortgrass state occurs. As with the western wheatgrass model, this transition is considered likely to cross a threshold only after climate change resulting in prolonged dry conditions. Without fire, fringed sage may increase with heavy grazing (McWilliams 2003b). Because the needlegrass/sedge/blue grama types occur in drier upland areas, we assumed that transitions to states dominated by conifers, tall shrubs, or Kentucky bluegrass were not likely.

Note: State-transition models that included the needleandthread type were not available from NRCS. A model was created based on community descriptions for the needleandthread / sedge / blue grama association at Theodore Roosevelt NP and other park units (Von Loh et al. 2000) and a combined model for the western wheatgrass and needleandthread potential climaxes presented in Kudray and Cooper (2005).

**Needleandthread / Blue grama / Threadleaf Sedge Type
Upland Sites with Coarse Soils**



States

Transition Types

Transition Agents

Possible for most sites

No Threshold Crossed

Transition Across Threshold

Potentially occurring after prolonged climate change

Threshold transition requiring long time and high effort or that is rarely likely

LIG, LTIG = (Long - term) intermittent grazing with long rest periods
SG, HSG: (Heavy) reoccurring seasonal grazing
SLG, HSLG: (Heavy) reoccurring season - long or continuous grazing
F/NF: Fire / No fire
CA: Cultivation or other conversion followed by abandonment
IN/R: Invasion / Exotic removal
D/LTD: Multi-year / Long -term (multi-decade) aridity
M/LTM: Multi-year / Multi-decade mesic conditions
PDR: Prairie dog removal or die-off

Figure B-15. State-transition model for NGPN needleandthread site types.

Upland little bluestem or big bluestem types (Figure B-16): Little bluestem communities occur extensively at Wind Cave NP and occur frequently in small patches at other parks. At Wind Cave NP and Devils Tower NM, these sites are present upslope of western wheatgrass types in poorer, drier soils with more gravel compared to the swales (Salas and Pucherelli 1998a; Cogan et al. 1999). At Theodore Roosevelt and Badlands NP, the little bluestem type occur at the edges, shoulders, and backslopes of draws, frequently in soils with moderate to high gravel content (Von Loh et al. 1999, 2000). At Theodore Roosevelt NP, these sites may occur where snow accumulation is higher or where little bluestem colonized after erosion. Cover is moderate to high in most sites (40-100%). However, at Agate Fossil Beds NM little bluestem sites are sparser communities on very shallow-soiled upslope areas, with low grass cover (USGS undated b).

At Wind Cave NP, a big bluestem type (with little bluestem found in low abundance) forms on steeper, rockier sites than the little bluestem types (Cogan et al. 1999). Transitions between dominance by big vs. little bluestem are unlikely (D. Uresk, USFS, pers. comm.), although we considered including such transitions as possible after long-term changes in precipitation. At Scotts Bluff NM and other units, another big bluestem type occurs in floodplains, and is not covered by this model.

In this model, the climax community under frequent fires and intermittent grazing is dominated by little bluestem (or big bluestem on some sites at Wind Cave) and sideoats grama, with relatively high litter. Under regular grazing on either the big bluestem or little bluestem types, abundances of blue grama, hairy grama, and threadleaf sedge increase. Prairie sandreed is often present in the little bluestem type described by the USGS NPS vegetation mapping, and may be a minor but important member of these states. Western wheatgrass and needleandthread may also be important locally. With regular heavy grazing, NCRS models for adjacent areas predict a new stable state dominated by short warm season grasses, threadleaf sedge, and fringed sage, with increased areas of bare ground. For NGPN parks, we did not model this as a threshold transition but predicted relatively easy recovery of little bluestem with reduced grazing, and no loss of little bluestem under prolonged drought (D. Uresk, USFS, pers. comm.). Because the bluestem sites occur most frequently on shallow soils and slopes, the model does not include a state associated with prairie dog towns.

At Wind Cave NP and Devils Tower NM, little bluestem sites often occur adjacent to or as patches in ponderosa pine forests and woodlands. These ecotones and savannas are covered in a separate model. As in the western wheatgrass type, encroachment by conifers into bluestem-dominated patches is unlikely in most areas away from the Black Hills. The model includes this transition because it is plausible for large patches of bluestem types at Wind Cave NP. At Wind Cave NP, a ponderosa pine/little bluestem type is widespread, and sites identified as little-bluestem grasslands often have some burned pine snags. With several fire-free decades, pine seedlings would establish and mature grasslands adjacent to tree patches, resulting in a savanna or woodland state that could persist with the return of fire. For these patches, both this and the foothills/savanna model are needed to cover major potential transitions. In addition,

encroachment of pine into little bluestem patches may occur adjacent to Fort Laramie NHS, and in localized patches at Badlands NP (Von Loh et al. 1999; USGS undated c).

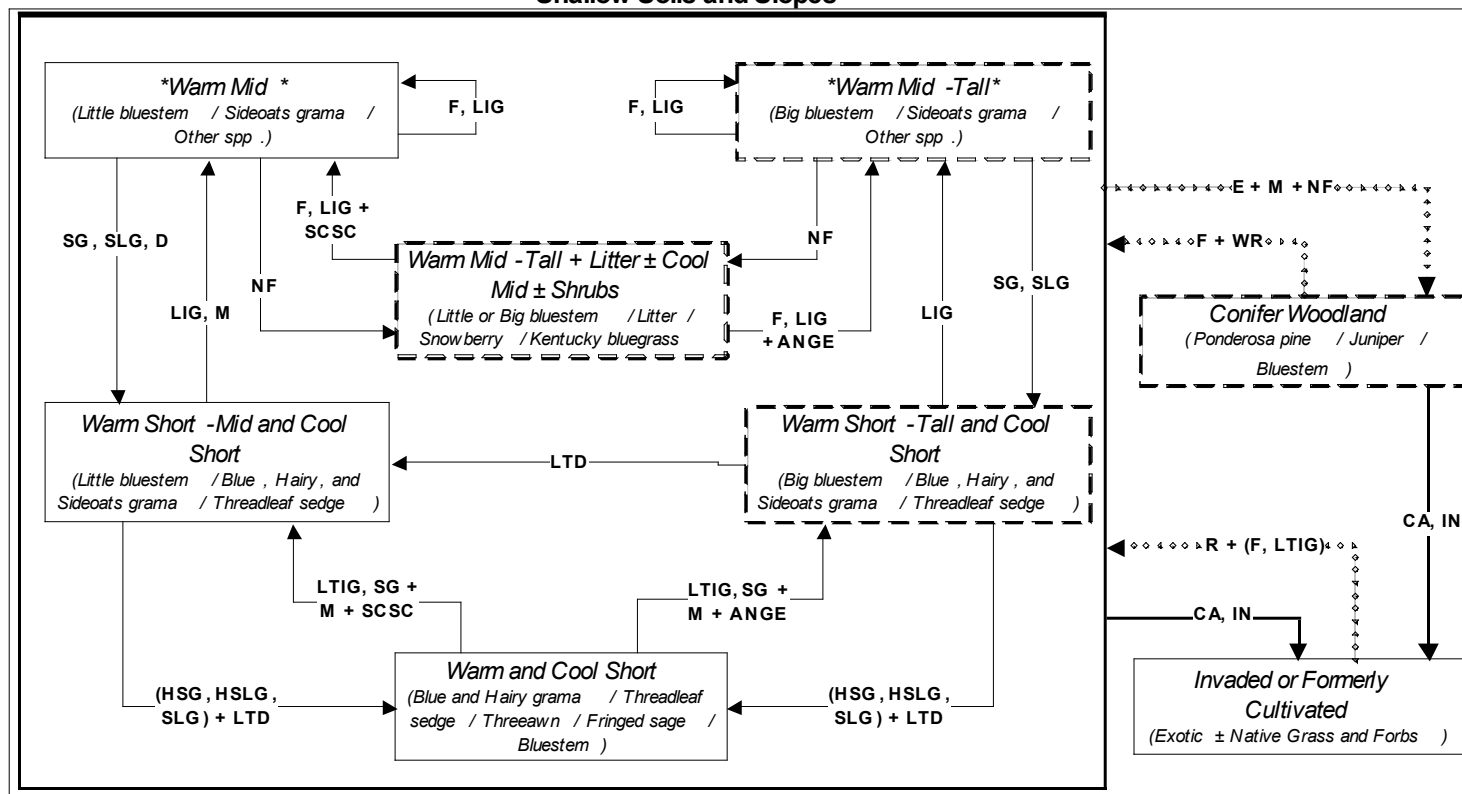
At Wind Cave NP and Devils Tower NM, little bluestem communities often are upslope or intermixed with western wheatgrass and Kentucky bluegrass types. In the absence of fire and under moister conditions, we assumed that Kentucky bluegrass might increase in the little bluestem stands. At Badlands NP, Von Loh et al. (1999) noted frequent occurrence of snowberry and ill-scented sumac in the little bluestem types. There, shrub density was expected to increase slowly without fire. However, we assumed that little bluestem would remain dominant, and that a transition across a threshold to a state dominated by Kentucky bluegrass was not possible for little bluestem types.

Note: In contrast to the available NRCS little bluestem models, we include a state of increased shrub or Kentucky bluegrass abundance. Although NRCS site descriptions for southwest SD include little bluestem / sideoats grama climax communities, these models treat needlegrass or needleandthread as dominant members that help define transition states. However, these species are rarely noted as important or regular members of little bluestem types in the NGPN parks (e.g., USGS NPS Vegetation Mapping program *a, b, c, d*; Hansen et al. 1984). Our model included similar states as the NRCS models, but we assumed these states were defined by increases in species other than needleandthread or green needlegrass.

Sandy Types (Figure B-17): This model applies to sandy sites in multiple NGPN parks, but does not explicitly cover the Nebraska Sandhills south of the Niobrara NSR. Sandy grassland communities occur extensively on flats, valley bottoms, and gentle slopes at Agate Fossil Beds and Scotts Bluff NMs. In these areas, sand sagebrush, rose, and yucca occur commonly at low densities. These species form sparse shrublands at Fort Laramie NHS and in sand hills of the south unit of Badlands NP. Sandy soils also occur in frequent small patches on upper portions of draws at Theodore Roosevelt NP, and at the edges of intermittent drainages in Badlands NP.

Under pre-settlement grazing and fire regimes, these sites are dominated by mid-tall warm and cool season grasses, including prairie sandreed, needleandthread, sand bluestem, hairy grama, and little bluestem. (At Theodore Roosevelt NP and intermittent drainages of Badlands NP, sedges may be more prevalent and the bluestems absent or localized.) Vegetation cover is low to moderate (< 60%) with low forb abundance and moderate litter build-up. Scattered soapweed or sand sagebrush is present on some sites.

Upland Little Bluestem or Big Bluestem Type Shallow Soils and Slopes



States	Transition Types	Transition Agents
Possible for most sites	No Threshold Crossed	LIG, LTIG = (Long -term) intermittent grazing with long rest periods
Potentially occurring in restricted conditions of moisture , topography , or adjacent states	Transition Across Threshold	SG, HSG: (Heavy) reoccurring seasonal grazing
	Threshold transition requiring long time and high effort or that is rarely likely	SL, HSL: (Heavy) reoccurring season -long or continuous grazing
		F/NF: Fire , No fire
		E/WR = Woody encroachment / Removal : brush or logging treatment
		CA: Cultivation or other conversion followed by abandonment
		IN/R: Invasion / Exotic removal
		D/LTD: Prolonged (multi -year) / Long -term (multi -decade) aridity
		M: Prolonged mesic conditions
		ANGE/SCSC : Big bluestem / Little Bluestem type

Figure B-16. State-transition model for NGPN bluestem site types.

Except in very sparse communities, litter would build up enough to carry a fire in 3-5 years without disturbance (Potvin and Harrison 1984). Similarly, moist periods with increased cover, followed by dry summer conditions, lead to sufficient fuels to carry fires. Prolonged periods without fire could allow temporarily increased density of shrubs, while fire decreases shrub cover and height. However, sand sagebrush resprouts strongly after spring or fall fires; eradication of shrubs by a single fire is unlikely (McWilliams 2003a), as is formation of dense shrublands in sandy sites when fire is excluded.

Under regular moderate-to-high intensity grazing, needleandthread and tall warm-season species are reduced. Sand dropseed, blue grama, and sedges increase as the community becomes dominated by short and mid-height warm-season species. With heavy re-occurring grazing, the site becomes dominated by bare ground, short grasses, cheatgrass, and annual forbs. Sand sagebrush is maintained or increased by moderate to heavy grazing (Gillen and Sims 2006).

As with other grassland types, we hypothesized that this type has high resilience in the NGPN (D. Uresk, USFS, pers. comm.). Only with a long-term drier climate would the site cross a threshold to a semi-permanent state characterized by bare sand, short grasses, and annuals. The model does not include a state associated with prairie-dog towns because few colonies are present in extensive sandy areas (Sidle et al. 2001).

Localized heavy disturbance by bison may remove vegetation cover. In the Nebraska Sandhills, prolonged drought may decrease vegetation density leading to blowouts (Sullivan 1994). Although extensive blowouts have not been noted in the NGPN parks, the resulting unstabilized state could occur on sandy slopes and ridge tops. As in the Nebraska Sandhills, such blowouts are likely to be sparsely vegetated and erodable until stabilized by blowout grass, lance-leaved psoralea and other forbs, sand bluestem, and sandhill muhly (Coupland 1992; Sullivan 1994). Sand bluestem may increase rapidly once the blowout is stabilized (D. Uresk, USFS, pers. comm.).

Note: In the Nebraska Sandhills, several models would be needed to cover major sandy site types (choppy sands, rolling sands, and dry valley; Burzlaff 1962). However, a single model was assumed to be adequate for sandy sites in NGPN parks (excluding areas south of Niobrara NSR) based on community descriptions in the USGS-NPS vegetation mapping.

Warm and Cool Season Mid -Height to Tall Grasses as Baseline /
"Climax" Dominants : Sandy Upland Sites

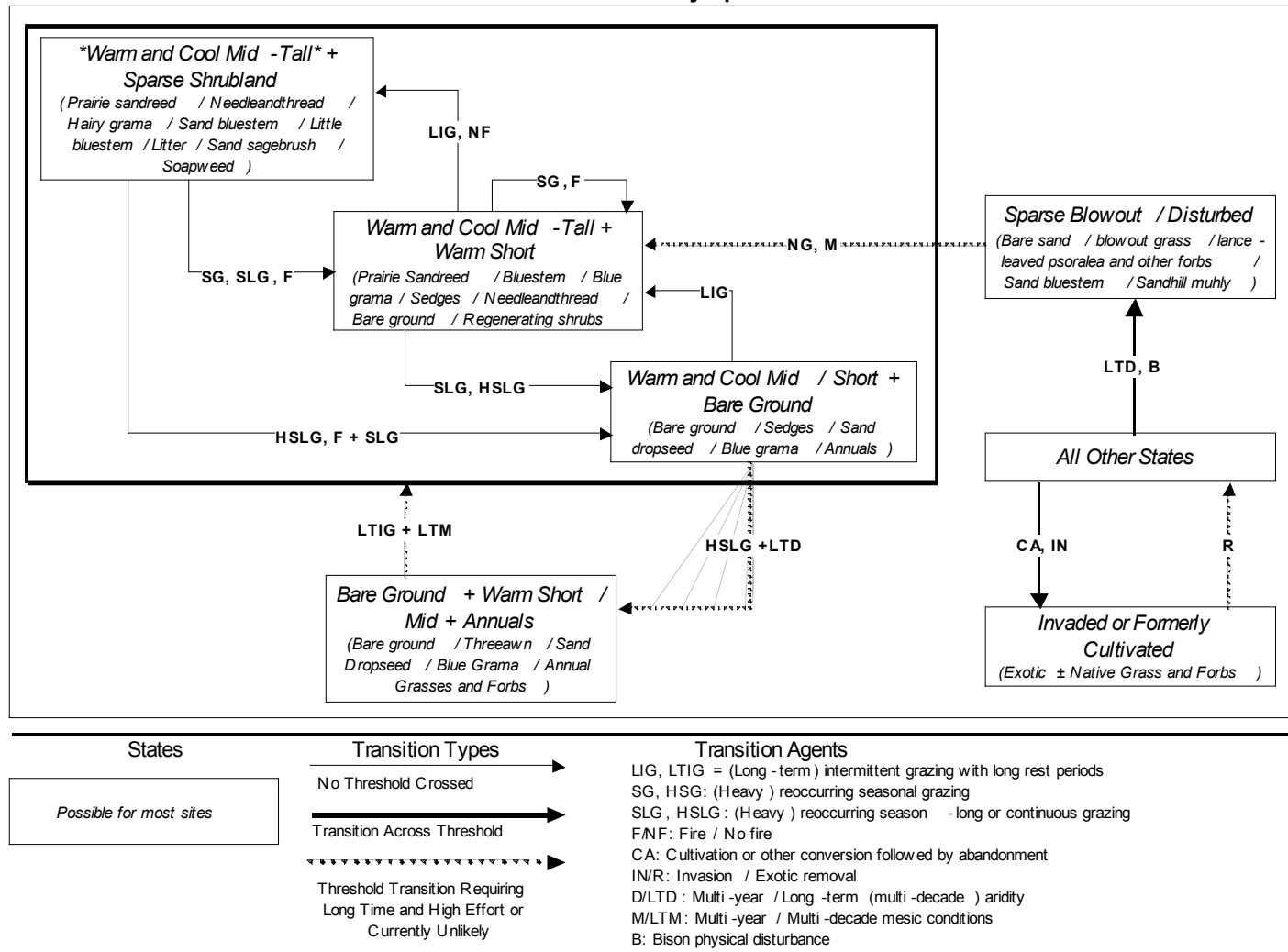


Figure B-17. State-transition model for NGPN sandy site types.

Northern Mixed-grass Prairie and Foothills: Woody Types

Although grasslands are the dominant cover type in most NGPN parks outside of the Black Hills, these parks also support woody types, including upland shrublands, woody draws dominated by deciduous or coniferous trees and shrubs, and riparian shrublands and forests. Numerous studies have examined the types of woody communities present in the NGPN area (Nelson 1961; Hansen et al. 1984; Girard et al. 1989). Topography, landform, and hydrology determine whether sites can support woody-dominated communities. Woody types are limited to mesic sites, such as swales and depressions, terraces and cliff bases in steep topography that receive higher run-off, steep north- and east-facing slopes, steep draws and drainages, and floodplains and riparian zones. In particular, these sites have higher soil moisture “because of one or a combination of the following factors: run-in from adjacent uplands, springs or seeps from through-flow of upper topographic positions, interception of the water table, decreased evaporation, flooding, and/or increased snow catch” (Girard et al. 1989:2).

Fire certainly affects the condition of these woody types, but the model of “no fire = woody expansion” is too simplified for the NGPN area even on a time scale of several centuries. The “no fire” model does not capture the major current patterns in the western NGPN grasslands except in ponderosa pine foothills and the Black Hills. In most of the NGPN away from the Black Hills, the loss or degradation of some woody types is of highest concern, rather than woody encroachment into grasslands. The increased occurrence of woody types in this region is due to tree plantings in rural and developed areas rather than reduced fire frequencies or grazing (Rumble et al. 1998). (Exceptions to this include potential encroachment by pine and eastern red-cedar at Scotts Bluff NM – covered by the foothills model - and larger scale encroachment by eastern red-cedar at the Missouri NRR and Niobrara NSR – which are not covered by current models.) Although woody types make up ~1% of the northern Great Plains landscape, they are of disproportionately high ecological importance. For example, woody patches support species that would be absent or less common in adjacent grasslands, and provide important resources (food and shelter) for predominately grassland species (Sieg 1988, 1991). Moreover, the riparian or mesic-upland sites in which these types occur are vulnerable to invasion by Kentucky bluegrass and other exotic species. These sites may be launching pads for invasion into adjacent grasslands.

We created several models to cover the major woody-dominated site types, including: a) sites dominated by big sagebrush (predominately benches at Theodore Roosevelt) or silver sagebrush (moderately open floodplain shrublands); b) other shrubland types of uplands; c) deciduous woody draws; and d) juniper-dominated woody draws. Additional models are being developed for riparian woodlands. As noted previously, state-transition models attempt to place highly heterogeneous parks with few clear boundaries between vegetation types into a few general categories or states. This contrast between simple models and complex reality is extremely high for woody types that occur both as large patches and in small patches of <100 m² ha in swales or as a woody stringer transitioning into grasslands in the upper ends of drainages. Such heterogeneity is highest at Theodore Roosevelt NP, where interspersed woody communities currently make nearly as much of the landscape as grasslands (35 vs. 40% of the park).

Several shrublands or sparse shrublands are included in other models are or not currently modeled. Sparse sand sagebrush stands are covered in the sandy grassland models. Rubber rabbitbrush occurs primarily as a weedy species in disturbed roadcuts and slumps at Theodore Roosevelt NP. Long-leave sagebrush occurs as part of sparse badlands vegetation. Rabbitbrush and long-leave sagebrush are not covered by these models.

Rocky Mountain Juniper Draws and Slopes (Figure B-18)

Woodlands dominated by short (3-6 m) Rocky Mountain juniper trees are present at Theodore Roosevelt and Badlands NPs and Scotts Bluff NM. Eastern red cedar dominates some woodlands in the Niobrara NSR area (Kantak 1995), and occurs in some portions of Scotts Bluff NM, mostly as a result of past plantings (USGS undated *d*). Hybrids between the two species occur at Badlands NP. Woodlands of Rocky Mountain juniper occur as a topographic climax in locations with higher moisture availability and usually occur on poorly developed clay, loamy, and scoria soils susceptible to erosion and mass slumping. However, the site characteristics vary somewhat among parks. At Theodore Roosevelt NP, juniper woodlands are limited to steep north facing slopes on “scoria”-capped clay buttes, sometimes forming dramatic contrasts with adjacent slopes. Juniper also occurs at upper edges of north-facing green ash draws. At Badlands NP, these woodlands occur in steep dry draws of all aspects, as well as ledges at the tops of tables and buttes. At Scotts Bluff NM, juniper woodlands occur on steep north slopes and in steep draws. In the Northern Great Plains, juniper-dominated stands can also occur as a seral stage on floodplains (Girard et al. 1989). At these parks, a ponderosa pine / Rocky Mountain juniper type occurs rarely but is more common in adjacent areas (Girard et al. 1989).

Rocky Mountain juniper stands appear to be stable, with juniper usually present as seedlings, saplings, and small trees (Ralston 1960; Nelson 1961; Girard et al. 1989). Numerous shrub species are present, but occur in low density once the juniper canopy closes partially. Green ash may be present in small moist microsites and dominate patches adjacent to juniper stands.

During a summer study at TNRP, north slopes dominated by junipers were similar to south slopes without junipers in moisture retention rates following rainfall (Ralson 1960). However, juniper stands had lower evaporation rates, lower daily maximum temperatures, and higher minimum temperatures than other sites. Stands dominated by juniper vs. green ash may fall along a gradient of environmental conditions. In most juniper stands, green ash occurs on moist microsites as a minor element of juniper stands. In a few juniper stands with higher soil moisture and lower evaporation rates, ash could become codominant or dominate the stand. Ralston (1960) predicted that ash would take over one juniper stand he sampled, a stand on an east slope with an upslope butte that provided shade and run-off. However, on most north-slope juniper stands at THRO, he speculated that periodic drought would prevent succession to ash dominance.

Understory development varies with juniper cover and perhaps environmental characteristics. Stands examined by the USGS –NPS Vegetation Mapping Program at Badlands and Theodore Roosevelt NP and Scotts Bluff NM typically were dense, (40-90% overstory cover), with low cover of shrubs (5-15%), graminoids and forbs (particularly littleseed ricegrass, with ~5% average cover at Badlands NP), and moss and lichens. Yellow sweetclover added 9% cover in Badlands NP stands examined by Sieg (1991). In juniper stands of western SD and southwest ND, ricegrass cover increases from early (2% average cover) to late (17% average cover) seral stages, even though juniper basal area and presumably canopy cover are highest in the late seral stage (Uresk et al. 2008). Somewhat counter intuitively, the highest cover of ricegrass appears in late seral states rather than in more open mid-seral stands (D. Uresk, USFS, pers. comm.). At Theodore Roosevelt NP, Hansen et al. (1984) reported average cover values of 17% for shrubs, 69% for ricegrass and other graminoids, 9% for forbs, and 72% for mosses and lichens. Nelson (1960) reported similar results in the THRO area. These studies do not report tree density in comparable ways, so it is unclear whether high understory and moss cover at THRO are due to canopy openness, more mesic conditions, or other factors. In addition, juniper had been cut in most THRO stands for fence posts prior to park establishment (1947), potentially allowing increased understory development and increased occurrence of green ash (Ralson 1960). Although occurrence of green ash in these stands may have increased historically after logging of junipers for posts, all successional states are still dominated by juniper (Hansen et al. 1984; Girard et al. 1989).

Information in fire return intervals or other processes affecting transitions among states was not available specifically for juniper woodlands in the northern Great Plains. Sites probably take 50-100 years to reach a mature state. Fire frequency estimates in juniper and juniper-pine forests of the western U.S. range from 35 to several hundred years (Scher 2002). Only larger diameter trees can survive even light surface fires. Otherwise juniper is killed by most fires, and does not resprout (Scher 2002). Presumably, fires in adjacent grasslands often would not burn into juniper stands which occurred on rugged north slopes or ledges protected from fire, and had little or no ground fuel. Rocky Mountain juniper does not begin producing berries until it is at least 10 years old (Noble 1991). Very light fires could thin the juniper stand but leave it in an open woodland state.

We speculate that transitions among juniper-dominated woodlands, savannas, shrublands, and grasslands fit into two categories. First, there are transitions on sites where Rocky Mountain juniper forms the topographic and edaphic climax. On mesic, steep, shallow-soiled slopes, a single localized fire will kill most junipers, but some will survive in patches or outcrops missed by the fire. The site may stay in a prolonged early seral condition dominated by grasses and shrubs, but junipers will slowly reseed and regain dominance (Ralston 1960). Repeated fires could kill the juniper seed source within a stand, leading to a semi-permanent shrubland, grassland, or exotic-dominated patch. However, the site remains capable of supporting junipers once seeds are dispersed into the site, particularly because the shallow soils would not develop thick enough grass cover to prevent juniper establishment.

Juniper Woodlands **Rocky Mountain Juniper and Hybrids with Eastern Red Cedar**

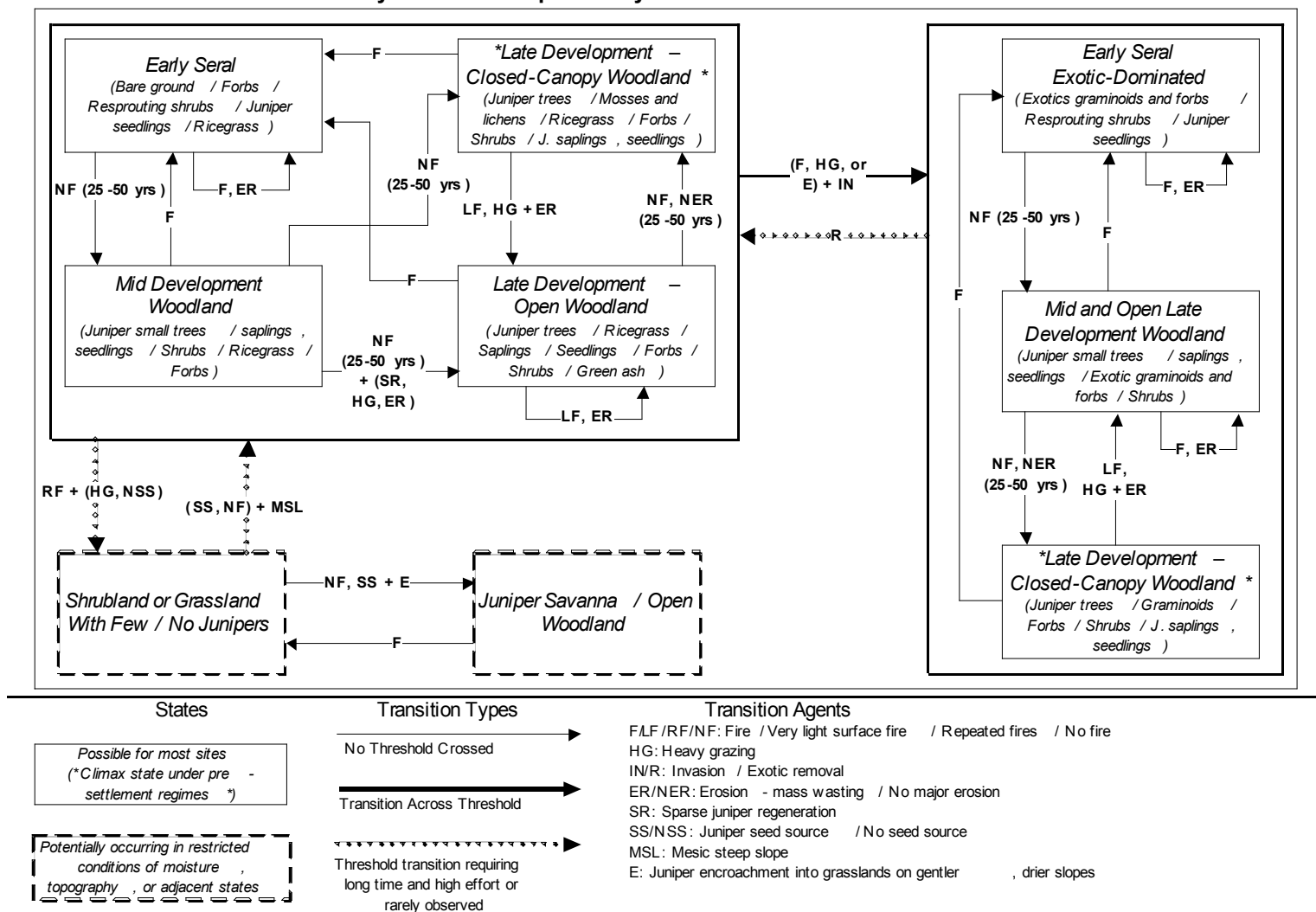


Figure B-18. State-transition model for NGPN juniper woodlands.

Second, there are transitions where a grassland type is the stable state with frequent fires. These sites may occur on slopes adjacent to juniper sites, and have better developed soils, have fewer barriers to fire, and occur on warmer and drier exposures. Junipers may slowly colonize sites adjacent to woodlands and form a savanna or open woodland state. However, unlike the core woodland state that stays in a juniper-dominated pathway, the savanna state returns to grassland after fire (Wakimoto and Willard 2004). Widespread juniper encroachment has not occurred in the NGPN, except for eastern red cedar expansion in the southern and eastern edge of the network. Juniper encroachment might become a bigger problem in this area if there was a prolonged significant increase in precipitation.

We do not model browsing as an important transition agent. Junipers are sometimes browsed heavily, potentially reducing tree vigor (Noble 1990). However, in the NGPN, ungulates browse Rocky Mountain juniper lightly or not at all (D. Uresk, USFS, pers. comm.). Even if browsing on saplings and seedlings was high enough to reduce regeneration, this would not be sufficiently severe to affect the structural pathway. Rather, continued heavy browsing would be inhibited by the topography and intertwining juniper branches.

Rocky Mountain juniper woodlands occur on shallow-soiled sites. Heavy use by bison and other ungulates can increase erosion (Noble 1990; Sieg 1991), both directly and perhaps by reducing moss cover. Large slumps would remove junipers and move the stand to an open woodland state. Nelson (1961) noted that dwarf junberry, buffaloberry, and other shrubs often formed dense patches on surfaces exposed by slumps. We assume that eroded sites would be at high risk of invasion. However, in contrast to deciduous woodlands in this region, Kentucky bluegrass and *Bromus* are minor elements or absent from existing juniper woodlands (Nelson 1961; Hansen et al. 1984; Girard et al. 1989; Von Loh et al. 2000), although at Scotts Bluff, cheatgrass was noted as being present in open areas with loose soils (USGS undated *d*). Potentially, these species could invade more juniper stands after fire or bison disturbance. With time, regenerating juniper or shrubs would likely shade out the exotics. Yellow sweetclover sometimes is the dominant herbaceous species in juniper woodlands (Sieg 1988; Larson et al. 2001), but still has low cover (10%). It is speculative whether sweetclover affects littleseed ricegrass or stonyhills muhly, the primary native grasses of juniper woodlands. Yellow sweetclover would decrease as juniper cover increases, but could dominate the stand after fire. Its seeds are long-lived and stimulated by fire scarification (Sullivan 1992). Further discussions are needed to determine if our model should include a juniper/exotic association as a separate pathway.

Note: The specified years required for successional juniper transitions are speculative. The ponderosa pine/juniper type is rare at Badlands NP and Theodore Roosevelt NP, but is more common in surrounding ridges, and is present at Scotts Bluff NM. We do not know whether these sites fit into the foothills model, or whether pine invasion of juniper stands should be added to this model.

Green Ash Draws (Figure B-19)

At Theodore Roosevelt NP and adjacent areas, narrow woodlands dominated by green ash are common and visually obvious, although they make a small part of the total area of the landscape. In these sites, green ash forms open- and closed-canopy woodlands with American elm, chokecherry, snowberry, and other shrubs. These woodlands form long stringers in upland draws, and occur on moderately steep north and northeast facing slopes (Von Loh et al. 2000). Green ash draws also occur at Badlands NP, east of Wind Cave NP, and adjacent to Fort Union Trading Post NHS. At Badlands NP, green ash woodlands also occur at the base of sand hills, where seeps and springs form at the boundary between sand and clay soils (Von Loh et al. 1999). Green ash is also present in floodplain forests, which are not a focus of this model. Like some green ash draws, some ash stands on steep slopes at Knife R. Indian Villages NHS may be an extension of riparian forests transitioning into upland grassland

Although <1% of the northern Great Plains landscape is comprised of green ash woodlands, these sites are of high ecological interest and management concern (Hodorff et al. 1988; Irby et al. 2000). Because the surrounding landscape is mostly grassland, these upland woodlands are important structural elements, providing important habitats for wildlife (see brief review by Lesica 2003). For example, >50% of bird species present in these sites require woodland habitats the woodlands may be important migration stopover areas (Hodorff et al. 1988; Rumble and Gobeille 1998). Trees in these draws are likely to provide important roosting habitats for bats, and the moist ground conditions and high deciduous litter are likely to support higher shrew densities than surrounding grasslands (R. Gitzen, pers. obs.). The draws are used heavily by elk and deer during the summer (Sullivan et al. 1988; Jensen 1992), although deer browsing is low in stand interiors (Irby et al. 2000).

American elm is co-dominant in many green ash draws (probably the more mesic sites; Girard et al. 1989). Rocky Mountain juniper and box elder occur as minor species. These woodlands generally have a shrubby border, forming a stairstep of habitats: grasslands; border of low shrubs (snowberry, skunkbrush, buffaloberry); border of taller shrubs (chokecherry, American plum, serviceberry) and ash saplings; and green ash woodland (Girard et al. 1989). Undisturbed stands often have closed canopies (70-100%; Rumble and Gobeille 1998; Von Loh et al. 1999). They are multi-layered, with an ash/elm overstory, a sapling/ shrub layer (dominated by ash and elm saplings, chokecherry, snowberry, rose, and service berry), and a herbaceous layer of forbs, grasses, and sedge (Hodorff et al. 1988). Reported average herbaceous cover varies widely (10-100% cover). Bedstraw, poison ivy, sedge, and Kentucky bluegrass (on lower and toe slopes) are abundant. Litter may cover much of the ground in undisturbed stands (65-95% cover, Irby et al. 2000).

In the northern Great Plains outside of parks, green ash draws have been considered imperiled habitats due to effects of heavy livestock use (Nelson 1961), possibly in conjunction with disease, drought, and wood cutting (Boldt et al. 1978). The shade and forage of these mesic sites leads to high trampling, compaction, reduced water infiltration, and browsing by cows. This reduces height of saplings and tall shrubs, and reduces or eliminates regenerating ash, elm, and

tall shrubs (Boldt et al. 1978; Uresk 1987). Water stress due to severe prolonged drought, reduced infiltration, and lower water tables, may cause high mortality of mature trees in the Great Plains (Albertson and Weaver 1945). Drought may interact with disease to produce canopy dieback (e.g., Lesica 2003). As mature trees die and are not replaced, the woodlands become increasingly open, with scattered large trees and understory regresses to low shrub dominated state characteristic of early seral conditions (Rumble and Gobeille 1998).

In mesic, productive sites such as these, risk of invasion is high (Stohlgren et al. 1999; Larson et al. 2001). Still, there are mixed reports about the current status of invasive species in green ash draws within NGPN parks. Kentucky bluegrass is an important grass in these draws, probably reflecting their mesic environment and history of livestock grazing prior to park establishment (Nelson 1961; Hansen et al. 1984; Butler and Trammell 1995). At Theodore Roosevelt NP, drainages and river bottoms are pathways of infestation by leafy spurge and probably other species (Anderson et al. 1996). Butler and Trammell (1995) reported that many green ash draws in the south unit were infested with leafy spurge. In contrast, leafy spurge occurred in only 2 of 12 stands sampled by Irby et al. (2000) in the south unit, and was absent from all stands in 1994 and 1996. Although Larson et al. (2001) did not report frequency of exotics in green ash draws, they found relatively high occurrence in snowberry/chokecherry sites. In green ash draws at Theodore Roosevelt NP, percentage cover of exotic grasses and invasive forbs increased from 1985 to 1996 (Irby et al. 2000). Still, cover values remained low at the end of this period (e.g., ~3% average cover of exotic grasses and <1% cover of invasive forbs).

Similarly, we have a poor understanding of the potential effect of invasive exotics in successional transitions of green ash draws. Heavy grazing may lead to a dense sod of Kentucky bluegrass or other exotics which further inhibits seedling establishment (Nelson 1961; Lesica 2003). In this situation, as residual trees die, a site gradually converts to a shrub or exotic-dominated type unless grazing is reduced and green ash is replanted or able to regenerate naturally. We do not know whether high cover of Kentucky bluegrass would be sufficient to drive the stand along this pathway in the absence of heavy grazing, particularly in relatively healthy stands of NGPN parks. For example, although nearly all stands sampled by Lesica (1989) with poor ash regeneration (0-3 seedlings per 100-m² plot) had $\geq 75\%$ cover of exotic grasses, high exotic cover could be a symptom of heavy grazing rather than a direct inhibitor of ash regeneration. It is also unclear whether leafy spurge infestation is likely to inhibit regeneration. Kentucky bluegrass is present but its cover (8-15% average cover documented by Hansen et al. 1984 and Butler and Trammell 1995; ~3% cover documented by Irby et al. 2000) likely is not high enough to hinder establishment of green ash seedlings. Butler and Trammell (1995) do not report whether tree seedlings were absent in two infested stands with 3-31% cover of leafy spurge. In contrast to green ash draws outside of the NGPN parks (see below), stands at Theodore Roosevelt and Badlands NPs have healthy regeneration (Irby et al. 2000) even though many sites (at least at THRO) were used for livestock grazing prior to park establishment in the early 1900s.

Exotic species exclude some native understory species in these draws. Across all stands sampled by Butler and Cogan (2004), uninfested stands supported 28 species that were absent in infested patches. However, compared to its effects in other community types, leafy spurge had lower effects on species occurrence and minor effects on total species richness of green ash draws. Irby et al. (2000) noted that exotics did not appear to be replacing native species in the interiors of green ash stands. Certainly, concern about exotic effects in these draws is justified. The slow, minor increase in exotics observed by Irby et al. (2000) could reflect initial stages of more significant invasions into green ash draw, or could foreshadow a large increase in exotics as fire and ungulate use disturbs these healthy stands.

In the absence of heavy livestock grazing and exotic infestation, disturbances rarely cause transition across a threshold to a different site type. Both ash and elm can reproduce successfully in mature stands. Seedlings and saplings are present if sites are in good condition (Hansen et al. 1984; Girard et al. 1989; Sullivan et al. 1989). Bison use is moderate or localized, and does not hinder woody regeneration inside the stands (Hansen et al. 1984). In low to moderate densities, elk do not hinder regeneration, based on studies 1-12 yrs after reintroduction at Theodore Roosevelt NP (Sullivan et al. 1989; Irby et al. 2000).

We know of no data-based estimates of pre-settlement fire frequency for green ash draws. Fires from adjacent grasslands could burn through these narrow stands, particularly under dry and windy conditions (Sieg 1997; Zimmerman 1981). However, because of the steep sheltered topography and moister conditions, we assume that fire return intervals would be >10 years assumed for adjacent grasslands. A range of fire intensities were likely, with some ground fires and many mixed-intensity fires. Even ground fires have can have effects ranging from low to high severities. Based on post-burn comparisons with unburned stands, Lesica (2003) estimated that ground fires caused ~5-80% mortality of mature trees in open stands of eastern Montana. Occasional stand-replacement fires probably occurred, particularly when moist productive growing conditions were followed by severe drought (LANDFIRE 2005b). Stands would remain green through most summers; replacement fires probably occurred mostly in late summer or fall. Because of the high fuel loads after vegetation cured, hot fires might have been likely (Sieg 1997).

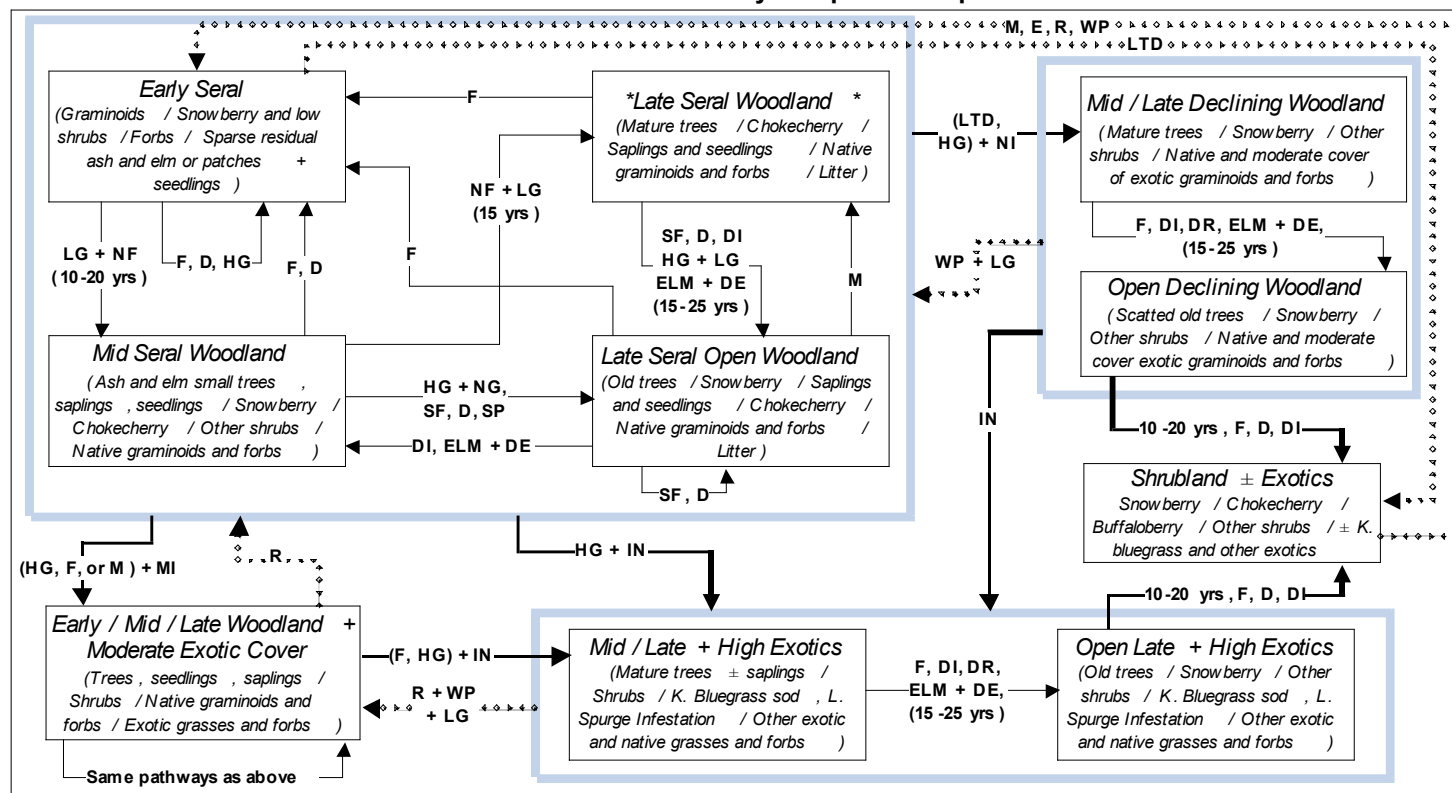
In the absence of long-term heavy grazing, prolonged severe drought, or invasive exotics, green ash stands are resilient. For example, stands at Theodore Roosevelt NP appeared healthy within a few decades after livestock grazing ceased (Hansen et al. 1984). Uresk (1987) noted slow increases in heights of green ash saplings on plots with a long history of intensive grazing. Some mature green ash and elm survive light ground fires; top-killed trees of both species resprout, with green ash probably showing slightly higher survival and a stronger resprouting response than elm (Coladonato 1992; Sieg and Wright 1996; Lesica 2003; Gucker 2005). Although their seed on the ground is destroyed by fire, reproductive individuals of both species produce high numbers of wind-dispersed seeds that could establish on burned sites in the absence of dense bluegrass sod or livestock grazing (Uresk and Boldt 1986; Lesica 2003). Resprouting and seedling establishment probably decreases and becomes slower during droughts and in the drier

western portions of the northern Great Plains (Sieg and Wright 1996; Lesica 2003). Prolonged drought could reduce or eliminate regeneration, delaying successional development (LANDFIRE 2005b) or producing stands with old trees and low shrub- or exotic-dominated understories (Nelson 1961).

However, in most cases, fires likely regenerated green ash stands (Girard et al. 1987). Green ash, the dominant tree species in these draws, is relatively short lived (50-100 yrs; Boldt et al. 1978; Hansen et al. 1984; Rumble and Gobeille 1998). In the absence of fire for >50 yrs, short-lived green ash and tall shrubs may gradually die, producing a somewhat more open stand with higher cover of low shrubs, graminoids, and forbs (Irby et al. 2000). We do not know whether long-term fire exclusion would eventually produce shrub-dominated stands similar to those resulting from heavy grazing. On average, stands sampled by Irby et al. (2000) in Theodore Roosevelt NP still had green ash saplings in the understory, despite the effects of fire suppression. When saplings are present, it seems likely that they would recruit to the canopy as mature trees die in the absence of fire. In 12 green ash draws, percentage changes in sapling density from 1985 to 1996 ranged from >100% increases to complete loss (Irby et al. 2000). Sharp declines of green ash saplings in some draws could be caused by localized heavy grazing, disease, more severe effects of drought on some sites than others (e.g., sites at the edge of the moisture gradient suitable for supporting green ash), or an interaction of these factors.

In NGPN parks where green ash draws are relatively healthy, fires are likely to still have a regenerating effect rather than causing a threshold transition. It is unclear what effects exotics may have on this pathway. If Kentucky bluegrass or other exotics dominate the post-fire herbaceous vegetation, they may inhibit seedling establishment (Lesica 2003). Speculatively, although resprouting density would be high after one or several fires in these park stands, each repeated fire could completely kill a few more mature trees that would not resprout, eventually leading to conditions similar to those produced by livestock outside of the park. In degraded sites with scattered mature, declining trees and high cover of Kentucky bluegrass, fire may do more harm than good, in terms of restoration (Lesica 2003). Without seedling establishment in these sparse stands, fires may simply push the stand further along the transition to a permanent shrubland state. A combination of mechanical treatments or fire, replanting, grazing reduction and perhaps exotic removal may be needed to restore degraded stands (Uresk and Boldt 1986; Lesica 2003).

Green Ash Draws
Mesic Draws and Moderately Steep North Slopes






States	Transition Types	Transition Agents
<div style="border: 1px solid black; padding: 5px; margin: 5px;"> <i>Possible for most sites</i> <i>(*Climax state under pre - settlement regimes *)</i> </div>	 No Threshold Crossed	LG/HG: Light or no grazing / Prolonged heavy grazing or heavy browsing HG + LG: Prolonged heavy grazing followed by recovery SUF/F/NF: Ground fire / Higher intensity fire / No fire
	 Transition Across Threshold	INMI/NI: Invasion / Low to moderate exotic increase / No exotics R/WP: Exotic removal / Tree planting
	 Threshold transition requiring long time and high effort	D/LTD: Prolonged (multi-year) / Long-term (multi-decade) aridity SP: Sparse overstory establishment D/ELM + DE: Disease / Elm co-dominant + Dutch elm disease E: Erosion extending draw upslope

Figure B-19. State-transition model for NGPN green ash woodlands.

Snowberry, chokecherry, and other deciduous shrubs common in green ash draws re-sprout and may show stable densities before and after fire (see model for shrub-dominated type, below; Sieg and Wright 1996). We have little information on fire effects on shrubs in healthy green ash draws; comparative and potential competitive responses of regenerating green ash and elm vs. regenerating shrubs have not been documented. However, Lesica (2001) suggested that chokecherry could facilitate establishment and growth of shade-tolerant ash seedlings by shading and reducing vigor of Kentucky bluegrass, by moderating microclimate, and by protecting seedlings from browsers. Shrub response after cutting of mature trees is slow and variable among species. Uresk and Boldt (1986) observed weak to moderate responses after partial overstory removal: snowberry gradually increased on harvested sites during years 1-6 after cutting; rose showed an initial increase that appeared to dissipate within 2 yrs; chokecherry was slightly denser on uncut sites. Cover of snowberry and chokecherry are inversely related (Voorhees and Uresk 1992). Along with basal area of green ash, contrasting percentage cover of *Prunus* vs. snowberry are key variables that discriminate among 4 seral stages identified by Uresk et al. (2008). *Prunus* cover is low soon after disturbance (4-8% cover), increases in mid-seral stands (~48% average cover), and starts to decline as stands reach a late seral stage (Uresk et al. 2008). Relative importance of snowberry is highest in the early-intermediate seral state or with heavy grazing (D. Uresk, USFS, pers. comm.; Nelson 1961; LANDFIRE 2005b), although cover may be low in some cases (e.g., ~1% snowberry cover in early seral stands sampled by Rumble and Gobeille 1998).

Nelson (1961) speculated that green ash was extending further into the uplands as draws and intermittent streams extended into uplands due to erosion. At Theodore Roosevelt NP, he noted that heads of draws could have lush cover of bluestem, or shrubs and Kentucky bluegrass. Between the draw head and the ash stands, dense cover of shrubs often were common (see multi-species shrub model). Portions of these shrub patches had abundant ash saplings. Inside the upper portion of the green ash stand, trees were dense and young (<35 yrs), while shade intolerant shrubs appear to be declining or dying as they were shaded. This suggested to Nelson (1961) that green colonizes up the draw into shrub patches as the draws erode into the uplands, leading to stringers from the eroding heads of draws down to intermittent stream channels to the Little Missouri River. Studies do not report whether trees also generally are colonizing the shrub border typical of green ash stands. We speculate that pattern observed by Nelson (1961) could be produced by long-term extension of draws, fire, and drought. Some fires likely burn hottest at draw edges and heads, dying out as they enter moister parts of stand interiors. Green ash saplings might colonize border shrublands during moister periods but die back during droughts. Finally, ungulate use often is highest at stand edges (Irby et al. 2000). All of these factors could interact to cause the shrub/woodland transition to be dynamic.

Several pathogens may affect tree composition and structure in green ash draws, although more research is needed to assess the magnitude of these effects. Dutch elm disease is a threat to mature elms in this region, and could change stand composition in sites where elm is co-dominant (Girard et al. 1989). However, we do not know if such changes have occurred or how likely these changes are likely to occur at Badlands and Theodore Roosevelt NPs. Because younger elm seedlings and saplings can survive in the presence of Dutch elm disease, elm could

persist as an understory tree (McBride 1973; Parker and Leopold 1983; Girard et al. 1989). If elm regeneration is not present, green ash and shrubs likely would increase following infection of stands with significant components of large elm. If ash and elm regeneration is poor, the disease would move stands along the transitions towards open woodlands and shrub-dominated states.

Perenniporia fraxinophila is a native heart-rot fungus that may slow tree growth and weaken limbs and trunks. Lesica et al. (2003) suggested that it was not a direct cause of canopy dieback, but that the fungi can contribute towards the overall decline of an ash stand caused by drought and heavy grazing. Drought-induced canopy dieback may create entry points for the fungus, and breakage of branches and trunks with stem decay reduces canopy cover. The fungus usually is not passed into stump sprouts (Lesica 2003). In the absence of heavy grazing or prolonged drought, the fungus probably would have minor effects on stand structure. Older ash trees commonly have heart rot.

Ash yellows, a systemic disease caused by phytoplasma, often causes ash to develop witches'-brooms. The disease reduces growth rates in ash of eastern North American forests and urban areas, causes crown dieback, and eventually kills some trees. It is widespread in the northern Great Plains, although forest pathologists do not know whether it arrived recently or has historically been present (Walla et al. 2000). In this region, incidence is highest in trees with heavy crown dieback (Walla et al. 2000), but we do not know whether it is a significant threat to green ash stands in NGPN parks or what transitions among states are likely.

Note: In southwest North Dakota, green ash draws may border and transition into tree-dominated states not covered by this model. Drier slopes of woody draws may be dominated by bur oak or a mix of ash and bur oak (Girard et al. 1989). Ground fires that kill green ash (Lesica 2003) often would not be lethal to mature oaks. Frequent fires and drought could favor oaks in these stands. However, bur oak is not reported to be an important component of green ash draws at Badlands and Theodore Roosevelt NPs. In drainages of the Black Hills foothills, green ash and elm occur with box elder and bur oak (Sieg and Wright 1996); these sites are not covered here.

In a few sites at Theodore Roosevelt NP and more commonly in the adjacent landscapes, quaking aspen dominates the upper portion of north slopes above green ash stands. Ash may take slowly take over these aspen stands in the absence of disturbance (Hansen et al. 1984, Girard et al. 1989). Because this aspen type is a minor element at Theodore Roosevelt NP (Von Loh et al. 2000), we have not included it in the model.

Although native ungulates may not have greatly affected stand structure in the recent past, increasing abundance of white tailed deer and elk could lead to higher impacts (Lesica 1989, Irby et al. 2000). Further discussion is needed with park staff and other experts to judge whether white-tailed deer are a high threat to continued ash regeneration in woody draws.

Big Sagebrush Uplands (Figure B-20):

Big sagebrush-dominated stands are widespread in eastern Montana and Wyoming, and in some areas of western North Dakota. However, the USGS – NPS vegetation mapping program in the NGPN identified shrublands dominated by Wyoming big sagebrush as a distinct vegetation type only at Theodore Roosevelt NP. At THRO, these shrublands occur in moderately deep soils on level benches and terraces 3-60 m above the Little Missouri River and tributaries (Hazlet and Hoffman 1975; Hansen et al. 1984; Von Loh et al. 2000). On drier aspects, the stands are restricted to the bottom of steep slopes where runoff provides moisture (Von Loh et al. 2000). The shrublands are moderately open (25-30% shrub cover) with western wheatgrass understories. In addition, a big sagebrush / spiny saltbush sparse shrubland is widespread on badlands, steep slopes, and ridges at THRO and throughout the badlands of western North Dakota and eastern Montana (Brown 1971; Von Loh et al. 2000). The big sagebrush model covers the bench and terrace shrublands, but not the badlands sagebrush – saltbush stands.

The big sagebrush model focuses on the effects of fire on sagebrush, and the effects of grazing and exotics on the understory layer. Big sagebrush is killed by fire and does not resprout. It re-establishes slowly from seeds from residual shrubs, from adjacent stands, and from the soil seedbank (Howard 1999). In Wyoming big sagebrush across the West, fires historically occurred at 10-70 yr intervals and were patchy, leaving residual patches that provided a seed source (Howard 1999; Baker 2006). Of 23 sites with big sagebrush stands burned by wildfires in the northern Great Plains, Wakimoto and Willard (2004) classified 20 as converted to grassland sites due to high shrub mortality. However, most sites had burned within the previous 10 years, and average cover of big sagebrush was still ~3%. Given the slow re-establishment of big sagebrush (see below), potentially most of these sites will return to a shrub-dominated cover type.

In eastern and central Wyoming and Montana, a 90 yr mean fire-return interval is hypothesized (LANDFIRE 2005a). Baker (2006) estimated that Wyoming big sagebrush stands burned with average rotations of 100-240 years, while mountain big sagebrush burned every 70-200 years. Presumably, the mesic benches on which sagebrush occurs at THRO burned infrequently (intervals 100 yrs) compared to grasslands on the landscape.

Post-fire re-establishment of big sagebrush is affected by seed availability (in the soil and from surviving plants), precipitation, competition from grasses and exotics, and grazing (Knight 1994). Across the ranges of Wyoming and mountain big sagebrush, re-establishment takes several decades in most cases (Welch and Criddle 2003). Baker (2006) concluded that Wyoming sagebrush density sometimes returns to pre-fire levels within a decade, but generally takes 50-120 years across its range. Seedlings may establish in pulses as the stand develops, with multiple cohorts in any stand but many years with no successful recruitment (Perryman et al. 2001). Because big sagebrush recovers slowly after fires, multiple fires within a few decades could allow other shrubs, grasses, or exotics to dominate the site (Knight 1994:103). Eventually, sagebrush could re-colonize the site if there are seed sources on the landscape.

Grazing was modeled as having little effect on the shrub component but grazing would alter the grass composition as in the grassland models. However, western wheatgrass would be protected somewhat by the mature shrubs and would remain important even under continued grazing. We expect that continued grazing in the sagebrush stands would reduce the grass fuel load, and decrease the risk that fires would carry through the stand.

Compared to sagebrush sites to the west of the NGPN, for THRO big sagebrush stands we included fewer alternate states and reduced complexity of interactions driving transitions among states. (See models for western big sagebrush systems in Knight 1994:105 and West and Young 2000:262.) In contrast to shrub-steppe areas of western North America, an interaction of exotics and fire frequency (i.e., cheatgrass cover increases the risk of stand-replacement fires) probably is unimportant in the THRO sagebrush stands. Graminoid cover, particularly of western wheatgrass, is high (70-100%; Hansen et al. 1984) in THRO big sagebrush stands. Historically, the mesic condition and topographic locations of these sites probably influenced fire risk more than the amount of fine fuels. Neither Von Loh et al. (2000) nor Hansen et al. (1984) report significant cover of exotic grasses in these stands. Presumably, heavy grazing and soil disturbance could facilitate invasion by exotic grasses (Knight 1994), but the basic stand structure or fuel load would not change greatly on these sites.

In many sagebrush-dominated systems, heavy grazing can also affect stand structure either by reducing grass competition, leading to increased sagebrush establishment and shrub density, or by trampling sagebrush seedlings so that successful reproduction occurs only under the shelter of mature shrubs (Beck and Mitchell 2000). Absence of fire combined with heavy grazing could lead to increased shrub density and encroachment into adjacent grasslands. However, none of these transitions are currently likely at THRO, where big sagebrush is at the edge of its range. Wyoming big sagebrush is more palatable than other big sagebrush varieties, and is less favored by heavy grazing (Howard 1999). More importantly, in this region, much of the precipitation occurs during the summer, favoring grasses that rapidly take up water at shallow soil depths (e.g., Cook and Irwin 1992; Knight 1994). Further west, winter precipitation favors sagebrush. If this hypothesis is accurate, significant expansion of sagebrush occurrence or density is unlikely in the NGPN unless there is a major change in precipitation seasonality.

NOTE: The core sagebrush states were created using Benkobi and Uresk (1996)'s seral stage model from Wyoming as a guide, but we combined their "early" and "late intermediate" states into a single mid-development state. In addition, we allowed grazing in the absence of fire to alter grass composition without significantly affecting the shrubs. Further discussions are needed with North Dakota ecologists to check our assumptions, particularly about the relative stability of sagebrush on these sites when grazing is heavy. (Big sagebrush stands measured by Hansen et al. (1984) at THRO had 18-42% cover of big sagebrush and 50-87% cover of western wheatgrass, indicating that that most of the four stands were in late seral development using Benkobi and Uresk's (1996) summaries from Wyoming stands as a rough guide.)

Big Sagebrush Shrubland Mesic Loamy Benches in Grasslands

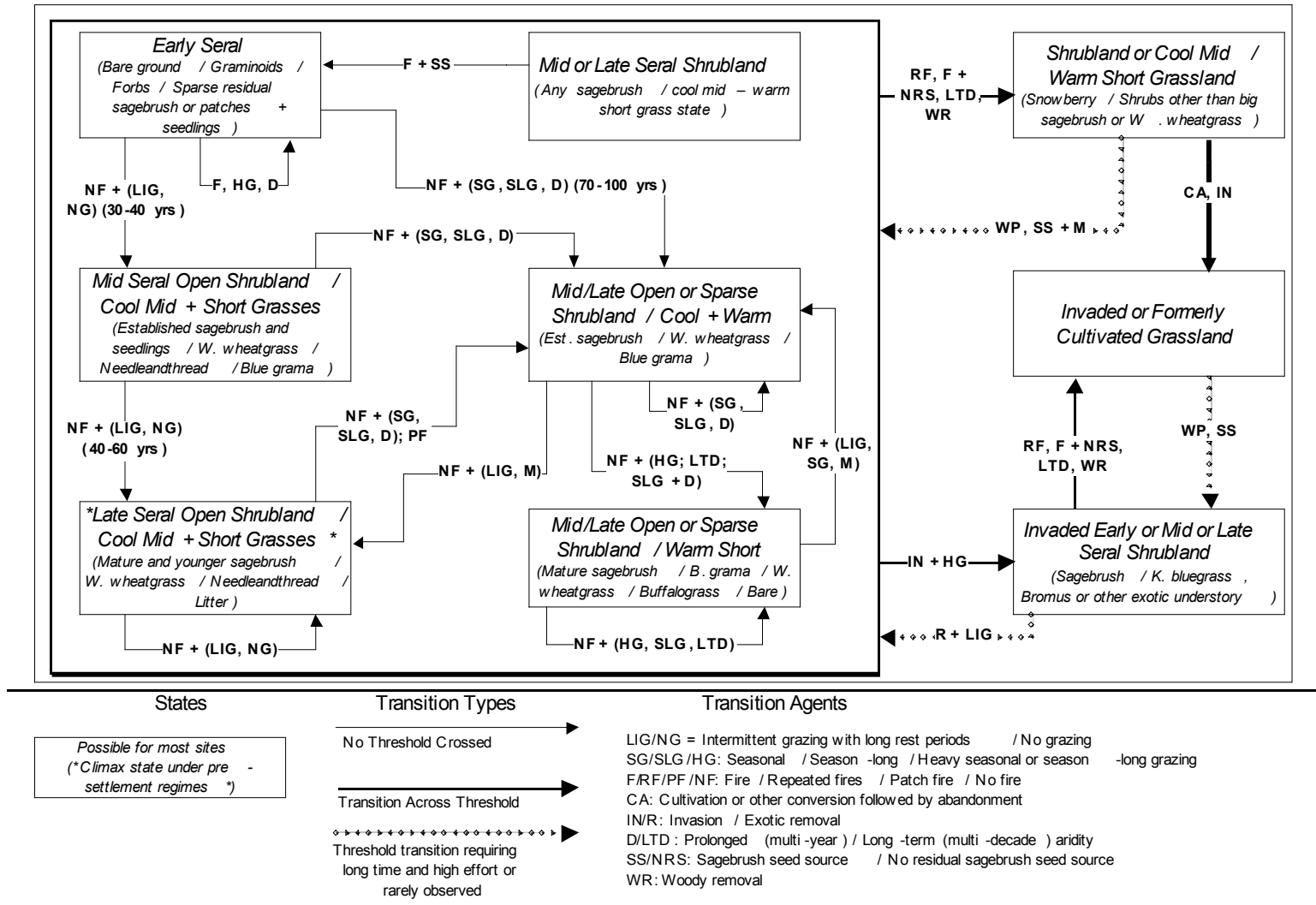


Figure B-20. State-transition model for NGPN big sagebrush shrublands.

Other Upland and Upland-Riparian Shrubland Types (Figure B-21):

This model covers sites where shrublands (other than sagebrush shrublands) are the long-term stable or climax community. Such patches are widespread in small patches across the region.

This model lumps sites dominated by several species:

- In nearly all parks, western snowberry forms dense patches in mesic sites, from small depressions to riparian zones.
- Chokecherry dominates a variety of sites at Wind Cave NP, including slopes, drainage bottoms, and rock outcrops. At Badlands NP, chokecherry is co-dominant with American plum in mesic draws, at the head margins of woodlands in draws, and in old oxbows and mesic soil slumps.
- Wind Cave NP supports some mountain-mahogany stands on steep limestone and sandstone slopes, and a few sites dominated by creeping juniper on steep east slopes of the Red Valley. Mountain mahogany is also present in or near Scotts Bluff NM as a minor, poorly developed community, while creeping juniper occurs on steep north facing scoria and gravel slopes at Theodore Roosevelt NP.
- Ill-scented sumac (skunkbrush) occurs on steep slopes at Theodore Roosevelt, mainly on upper scoria slopes. It occurs on ledges of very steep slopes, ridge tops, edges of draws and old oxbow at Badlands NPs.
- Silver buffalo-berry occurs in uncommon dense small patches in riparian zones at Badlands NP and at Theodore Roosevelt NP on upper north and east slopes and shoulders of upland draws, sometimes on the upper border of green ash draws.
- Sparse greasewood occurs in at least one patch at Theodore Roosevelt NP and in a few stands, mostly in alkaline flats at Badlands NP; these flats may be flooded occasionally and are slightly above the silver sagebrush floodplain.

Species dominant on some sites (particularly snowberry and chokecherry) may be a secondary or co-dominant species on other sites. Although edaphic characteristics or site histories can sometimes explain which species will dominate a shrubland (e.g., soil or moisture characteristics), ecologists often are unable to explain differences in species composition among sites. For example, in woody draws, soil characteristics did not discriminate between sites dominated by snowberry vs. chokecherry (Voorhees and Uresk 1992). Other differences in species dominance may be due to seral state, disturbance characteristics, random colonization and dispersal events, or undocumented soil and environmental differences. Therefore, our model does not delineate shrubland states based on which shrub is dominant. A generic model for shrublands dominated by any of these species is appropriate, as general effects of fire or grazing are similar for nearly all of these species. Other than big sagebrush and creeping juniper, most species dominating shrublands in the northern Great Plains will continue to resprout even after repeated fires (Higgins et al. 1989).

At times, it may be unclear whether a shrub-dominated site fits into this model vs. one of the other woody models. Some shrublands, particularly western snowberry and chokecherry patches, can occur in nearly all woody site types. Species may play different seral roles on different sites: for example, snowberry and buffalo-berry thickets may be stable on some riparian sites adjacent to sites where these thickets are a seral state succeeding to deciduous woodlands. Similarly,

semi-permanent shrubby patches may form a narrow transition from wooded draws (where the same shrubs would dominate an early seral state) to adjacent grasslands (Girard et al. 1989). Moreover, snowberry shrublands and buffalo-berry patches are present in both upland and riparian types (e.g., USGS-NPS Vegetation Mapping reports, Marriot and Faber-Langendoen 2000). These riparian shrublands may include sites in early seral, prolonged mid-seral, and long-term stable states.

Currently, our model does not include loss of shrubs and transition to a nearly pure grassland state due to repeated fires. Repeated or hot fires may reduce cover and abundance of these species, but eradication of shrubs from the site is unlikely without intensive management because of the strong re-sprouting response of most species. Shrub-dominated sites are limited to patches with higher soil moisture than upland grasslands, and a return to shrub dominance is likely even after hot fires. Conversely, although grasslands may support low cover of scattered shrubs, transition to a shrub-dominated state is unlikely in this portion of the northern Great Plains (D. Uresk, USFS, pers. comm.). Shrubland patches could transition to more open or grassland states, or to woodland states when shrublands are adjacent to green ash woodlands.

Further examination is needed to determine whether increased encroachment or loss of shrubs occurs more commonly near widespread woody types at Theodore Roosevelt NP, or is plausible network-wide with long-term changes in precipitation amounts over a time scale of several decades. For example, shrub invasion may occur more frequently within 100 km east of Badlands and Theodore Roosevelt NPs. Frank and Karn (2005) describe a site in central North Dakota that converted from grassland to a buffaloberry-snowberry shrubland between 1923 and 1970, and attributed this change to light or no grazing and lack of fire.

One potential major transition from pine forest to chokecherry shrubland could occur after high intensity fire in pine stands with a dense chokecherry layer. If all trees are killed but chokecherry re-sprouts vigorously, it could dominate the site (Cogan et al. 1999), presumably in high enough density to prevent pine regeneration. Currently, we include this as a transition in the foothills ponderosa pine model, but assume that pines would slowly colonize the site, so that the shrubland condition would be a prolonged seral stage. Conversely, some mountain mahogany stands have a ponderosa pine overstory at Wind Cave NP, and may be described better by the foothills ponderosa pine model.

Because creeping juniper does not re-sprout after topkill, severe or repeated fires in creeping juniper patches could be more likely to cause a transition to a grassland state. However, this transition is still unlikely. In the NGPN (mainly at Theodore Roosevelt NP), creeping juniper-dominated shrublands occur in small patches, on steep, north- or east-facing slopes, with low fuels other than the juniper mats. Although there is little data on creeping juniper recovery after fires in grasslands, ground fires usually do not kill all juniper stems on a site (Gucker 2006).

Some shrublands occur in small patches on very steep sparsely vegetated slopes or ledges on these slopes where they are protected from fire and grazing. These patches are likely to remain in the closed-shrubland condition semi-permanently.

Kentucky bluegrass and other exotics are likely to be present in most mesic shrublands. Often the grass/forb layer of the shrublands may support a mix of natives and exotics. In some sites, exotics may dominate the grass/forb layer, and may have dense cover in an early seral stage. At Theodore Roosevelt NP, leafy spurge infested some creeping juniper stands, producing a large decrease in species richness compared to infestation in other community types (Butler and Cogan 2004). However, it is unknown whether leafy spurge adversely affecting established juniper (e.g., through competition) or whether exotics would hinder shrub recovery after disturbance. We hypothesize that in most invaded shrublands, shrub cover will increase with succession, forming dense stands of snowberry or other shrubs that shade out most grasses. However, on some heavily grazed mesic sites, Kentucky bluegrass could form a dense enough layer to inhibit regeneration of shrubs even after grazing decreases.

Shrubland Types in Grasslands , Foothills , and Riparian -Upland Interface
Snowberry , Chokecherry , Serviceberry , Buffaloberry , Skunkbrush , Mt. Mahogany , or Horizontal Juniper Types

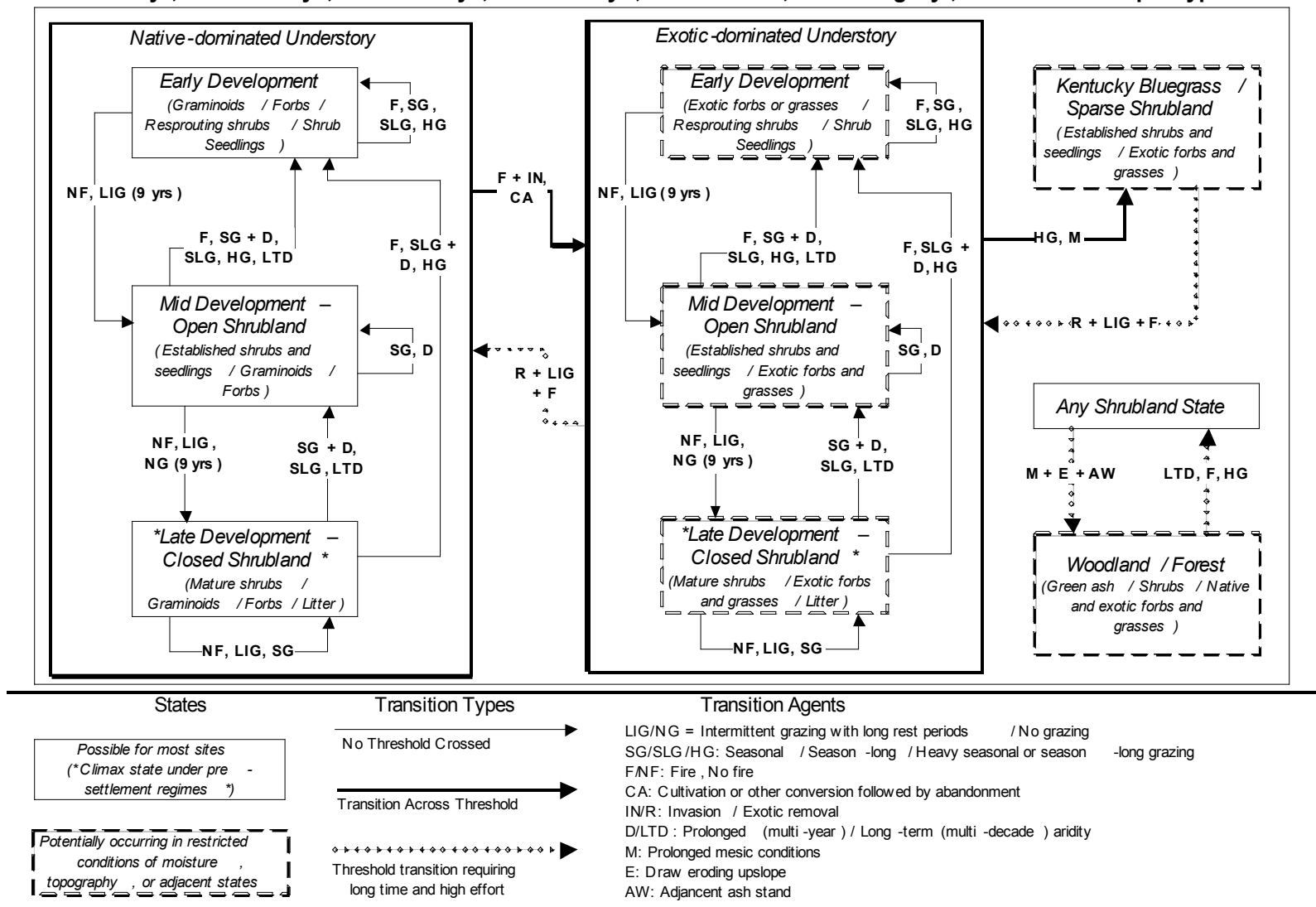


Figure B-21. State-transition model for other NGPN shrublands.

Floodplain and Riverine Riparian Communities

Most NGPN grassland parks border or straddle streams and rivers and support narrow to broad floodplains, or at least areas that were floodplains under historic pre-dam river flows. As a result, these parks support floodplain woody or moist herbaceous communities, which contrast greatly with adjacent upland areas in their productivity, composition, and other ecological characteristics. Away from the Black Hills, floodplains support the primary woodlands in the NGPN. Most animal species in the region use riparian areas, at least seasonally, and some require these areas (Knight 1994). Some species require the habitat structure of floodplain woodlands; for other species, floodplain woodlands and silver sagebrush stands are not required but provide important food, cover, and structural resources (e.g., cavities in live or dead cottonwoods). Floodplain communities are highly productive and are adjacent to the primary sources of free water in the region. Floodplain woodlands also provide shade and shelter. As a result, bison and other ungulates use these areas heavily.

In many ways, the condition of riparian and floodplain sites affects the species composition, diversity, and processes of the larger northern Great Plains ecosystem. Riparian zones link terrestrial and aquatic systems. Transfers of nutrients, sediment, and coarse organic matter (leaves to logs), and contaminants between aquatic and riparian zones affect both systems. For example, bank erosion in mature cottonwood stands adds enormous logs into rivers, but pollutants entering a river upstream may be deposited in floodplain communities. Riparian areas filter sediment and nutrients, and store water in alluvial soils that may prolong or sustain stream flow later in the summer (Knight 1994). In the NGPN, invasive species may initially colonize mesic, disturbed floodplain sites, and then expand upslope into drier areas.

Riparian and floodplain communities form a continuum of development driven by interacting effects of flood frequency and intensity, soil saturation and depth of water table, proximity to the channel, height above water level, sediment deposition, and ice scouring. In turn, these factors are controlled by flow levels, sediment availability, channel structure and substrate, channel erosion, and channel meandering which produces backwaters, old channels and different flow gradients and areas of deposition. As a result, sites in close proximity could support wet-meadow or riparian fringe herbaceous communities, early successional willow and cottonwood patches, woodlands, silver sagebrush stands, or grasslands and shrub patches. Proximate factors determining the dominant species on a site include duration of soil saturation, soil depth, soil texture, flood frequency, season and duration, water table depth, degree of ice scouring, soil oxygen availability, browsing, and fire (Knight 1994:47). Transitions linking these communities are driven by succession and changes in flooding and water table, which change the site type and the potential communities that can form. Changes in stream gradient, sinuosity, channel width-to-depth ratios, topography and floodplain landform, and soil type (Knight 1994:43) driven by stream narrowing/widening, meandering/channelization, and scouring/deposition produce various riparian landforms and resulting vegetation communities (Friedman et al. 1997:53-56). Biological factors such as beaver dams, grazing, dams, and irrigation withdrawals interact with these physical factors.

Modeling these complex dynamics is an ongoing effort. At this point, we have formed one complete conceptual model for silver sagebrush floodplain communities, and have begun literature reviews for further model development for floodplain woodland communities.

Silver Sagebrush Floodplain Shrublands (Figure B-22):

Silver sagebrush forms a floodplain shrubland type at Badlands NP, Theodore Roosevelt NP, Devils Tower NM, and Knife R. Indian Villages NHS. Silver sagebrush “flats” occur on floodplains and terraces slightly above the floodplain. Soils usually are deep alluvial deposits. Sites are prone to flooding, erosion, and deposition. Shrub cover is sparse to moderate (10-50%; Hansen et al. 1984; Von Loh et al. 1999); snowberry may form small dense patches or be co-dominant with silver sagebrush. In the northern Great Plains, stands of silver sagebrush are important habitats for sharp-tailed and sage grouse, pronghorn, and the sagebrush grasshopper (Howard 2002).

In sites covered by this model, some transitions are caused by relatively long-term changes in river channel and flood dynamics as well as vegetation succession. As a river channel erodes or shifts, sites occupied by silver sagebrush may transition to infrequently flooded upper floodplain areas, terraces, and eventually uplands. In the absence of flooding (e.g., due to dams or channel shifts), cottonwood stands develop into shrublands and grasslands (Friedman et al. 1997). Nelson (1961) outlined a successional trajectory of cottonwood as a pioneer, sometimes followed by green ash, transitioning into moister silver sagebrush stands, terraces with silver sagebrush, and finally into upland grasslands. Along the undammed Little Missouri River, many sites dominated by silver sagebrush had residual mature cottonwood and juniper trees (Nelson 1961). Our model also includes a direct transition from early seral states into shrublands by silver sagebrush. We do not know if this transition is likely, or if most of these shrublands have based through a woodland stage. Further discussion is need if Nelson’s (1961) trajectory captures the typical history of silver sagebrush stands.

This successional trajectory can be reversed. Shifts in the river channel and changing water levels may lead to active flooding, scouring, and deposition of sites that had been on the upper floodplain. Nelson (1961) noted that green ash may have been recolonizing some sagebrush stands as sites recovered from the 1930s drought.

These major changes in hydrologic regime form a backdrop for more rapid changes caused by fire, grazing, and individual floods. In contrast to big sagebrush, silver sagebrush tolerates flooding and can resprout after fire. Fire often may increase silver sagebrush density (Howard 2002). Burning in the spring may only topkill most plants, and resprouting will be vigorous if soil moisture is high. Burning under dry autumn conditions may kill >35% of silver sagebrush; with high fuel loads and a hot fire, mortality would be even higher (White and Currie 1983). In 10 of 11 sites studied by in the northwestern Great Plains, silver sagebrush remained present

after fire, although density decreased (Wakimoto and Willard 2004). On one site, fire killed all sagebrush and the site converted to a western wheatgrass type.

In stands of silver sagebrush, western wheatgrass is the dominant grass species (35-90% cover, Hansen et al. 1984) except after floods or heavy grazing. Green needlegrass may be a minor component, while blue grama may be favored by grazing and long flood-free intervals. Silver sagebrush tolerates flooding and deposition of material (Hanson and Whitman 1938). Recently flooded areas have high cover of bare ground between shrubs (Von Loh et al. 1999). Western wheatgrass can persist and recover in between floods, but frequent floods reduce or eliminate blue grama and green needlegrass (Hanson and Whitman 1938). On upper terraces that flood infrequently, blue grama may be more prevalent (Nelson 1961).

Moderate to heavy grazing may increase shrub density and decrease grass cover (Howard 2002). However, if grazing is prolonged and severe, cover of silver sagebrush will decline until grazing is reduced (Branson and Miller 1981). As in the western wheatgrass model, grazing would favor shorter grasses at the expense of needlegrass and wheatgrass.

Heavy prolonged grazing could allow exotics to increase in silver sagebrush stands (Montana Natural Heritage Program *undated*). Compared to other site types, silver sagebrush shrublands have average or higher than average frequency of occurrence of exotic species (Larson et al. 2001). Kentucky bluegrass often is abundant in these stands at Devils Tower NM, while *Bromus* spp. and leafy spurge may be abundant at other parks. At THRO, Butler and Trammell (1995) noted that leafy spurge formed dense patches from 10 m² to 2 ha in silver sagebrush floodplains and upland grasslands. There is a high risk of increasing exotic dominance on floodplains (Stohlgren et al. 1998; Larson et al. 2001).

Fire or flooding could also could reduce cover of native species and allow exotics to increase. In existing spurge patches, fire decreases seed germination. However, leafy spurge resprouts vigorously, and may be stimulated by fire if there is no herbicide treatment (Wolters et al. 1994; Simonin 2000b). In silver sagebrush patches invaded by leafy spurge, plant species richness is much lower than in non-infested stands (average of 9 fewer species, Butler and Cogan 2004). We do not know whether mature shrubs would be harmed as exotics increase in a stand, or whether infested patches would increase fuel loads and increase the risk of hot fires that could kill silver sagebrush. Although silver sagebrush can successfully establish from seed in grasslands (Romo and Grilz 2002), we assume that seedling establishment and survival would decrease in patches with high cover of leafy spurge. In this case, small-scale death of existing shrubs or high shrub mortality from a disturbance could lead to infestation by exotics.

Silver Sagebrush Shrubland Deep-soiled Floodplains and Terraces

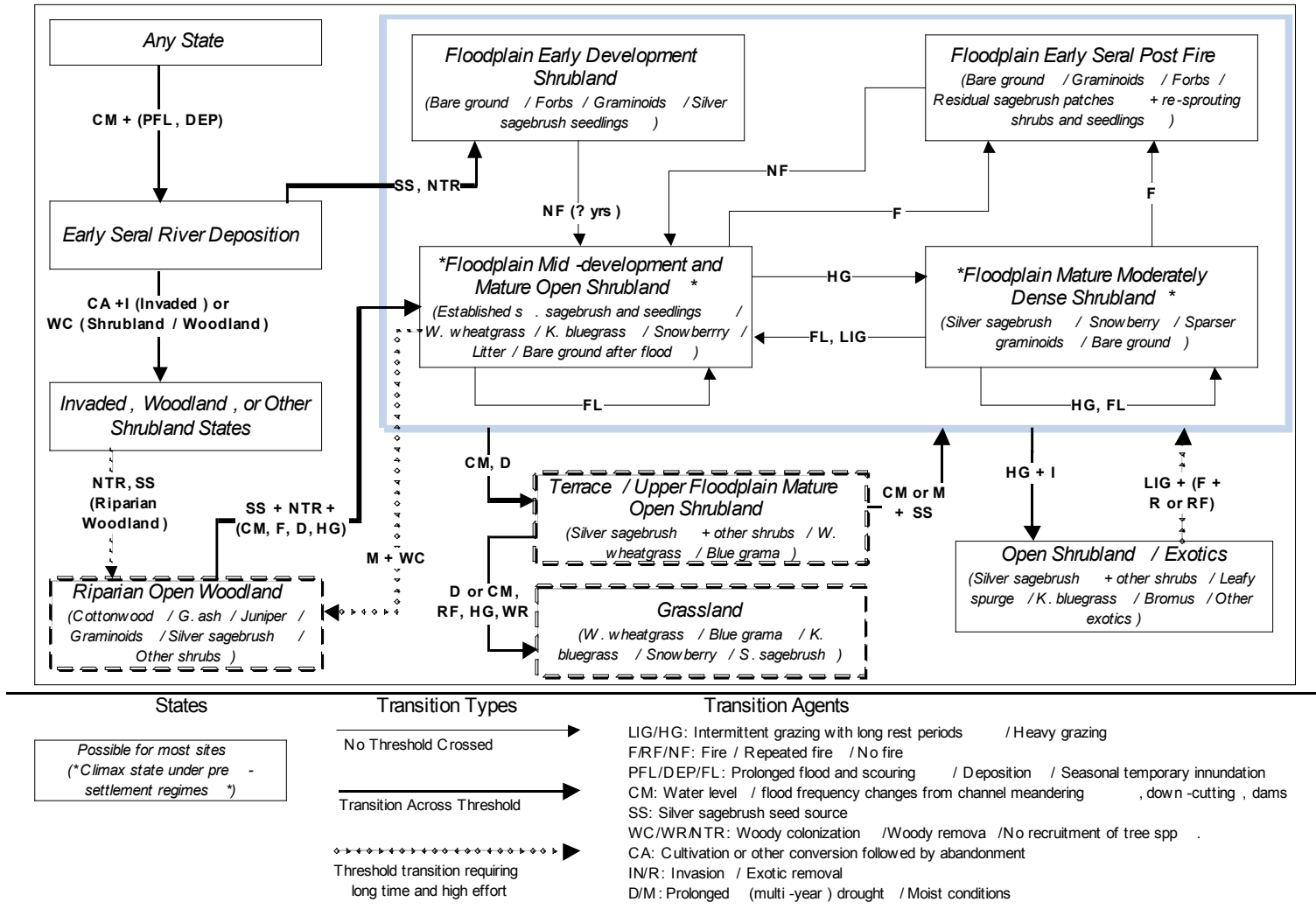


Figure B-22. State-transition model for NGPN silver sagebrush shrublands.

Floodplain Woodlands (Model not yet developed):

In the NGPN, floodplain stands dominated by cottonwood (*Populus deltoides*, the plains variety in most of the region), green ash, American elm, box elder, and Rocky Mountain juniper form the most significant woodlands and forests of the region outside of the Black Hills. Cottonwood is widely distributed, produces high quantities of wind- and water-dispersed seeds, and is the fastest growing tree in North America; it may grow up to 1.5 m in height per year for its first decade (Taylor 2001). However, cottonwood requires specialized conditions for establishment and survival (Figure B-23). Floodplain woodlands support tree- and shrub-dependent species absent from most other habitats in the NGPN. Individual mature cottonwoods provide unique habitat structure for cavity nesters in this region (Rumble and Gobeille 2004).

However, these deciduous habitats are being lost from large portions of the region (Boldt et al. 1978; Lesica 2003). Dams on most large rivers have reduced annual flooding. Large cottonwood stands on former floodplains are no longer regenerating; as scattered old trees in these stands decline and die, these sites convert to shrubland and grassland communities. Both woody draws and riparian woodlands are degraded by heavy use of stands by livestock outside of parks; inside parks, abundant elk, and deer may adversely affect regeneration in many stands. Change in precipitation and water tables due to climate change or adjacent land uses may further reduce regeneration. Some park management actions, particularly prescribed burning and treatment of diseased trees, may open stands further, potentially hastening their degradation.

Note: It is interesting to speculate about the historical effect of humans on floodplain woodlands and forests. Prior to white settlement in the Dakotas, the Hidatsa, Mandan, and Arikara tribes lived in semi-permanent villages on Missouri River terraces (e.g., at Knife R. Indian Villages NHS) and depended on these moist, fertile sites for growing crops (Ahler et al. 1991). In addition, these tribes used woodlands for winter shelter, fuel, and building materials. Conceivably such harvests may have affected significantly the structure of many floodplain woodlands. By ~1450, village populations along the upper Missouri River and tributaries may have been at a millennial peak due to favorable climatic conditions for agriculture (Ahler et al. 1991). For example, the Knife River reach of the Missouri River may have supported a population of 8,000-10,000 living in villages and dispersed houses, with each large communal house speculated to require several dozen trees for construction (Ahler et al. 1991:31). By the mid-1500's, circular earth lodges had replaced rectangular houses along the upper Missouri floodplains of North Dakota; each earth lodge required cutting ~150 trees of varying sizes (Ahler et al. 1991:42).

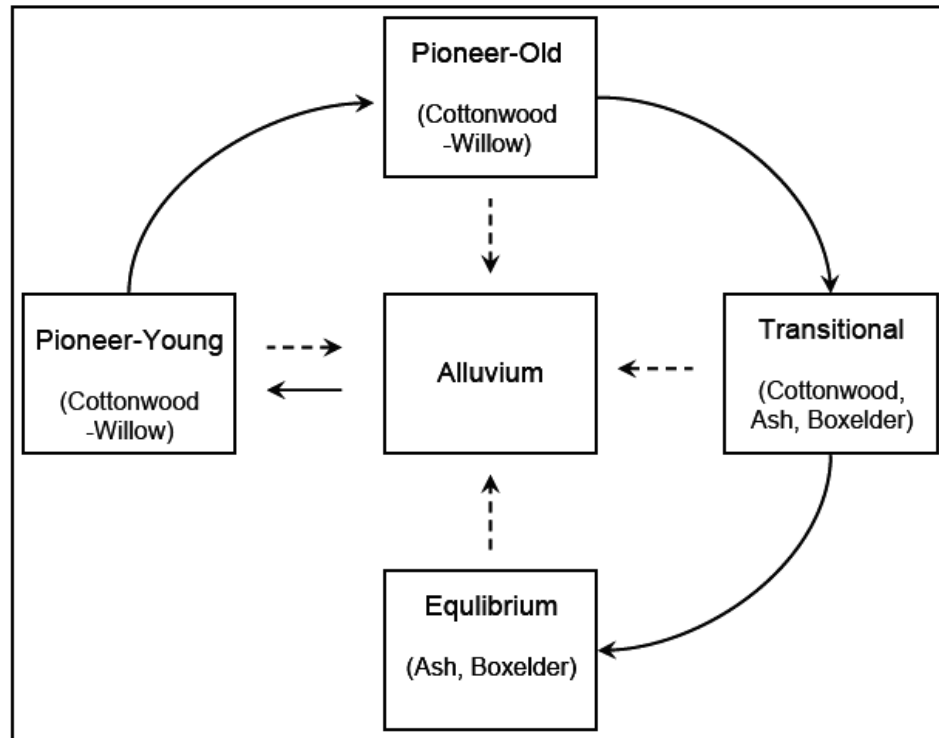


Figure B-23. Conceptual model of riparian succession. Succession is relative to the creation of freshly deposited alluvial surfaces. Solid arrows represent possible successional pathways and dashed arrows represented erosional processes. Source: Scott et al. (2005), who adapted model from Johnson (1992).

Black Hills Forests and Savanna

Four NGPN parks are in the foothills or interior of the Black Hills. Wind Cave NP and Devils Tower NM are at the edge of the Black Hills and support a mix of forests, woodlands and savanna, and grasslands. Jewel Cave NM and Mount Rushmore NMEM are in the interior central Black Hills – Jewel Cave is in the Limestone Plateau portion of the Black Hills, and Mount Rushmore is at the outer edge of the granitic Central Core. To model forest-structural states, we considered three general site types. The savanna / foothills model covers the grassland / forest transition at Wind Cave NP and Devils Tower NM. Although Scotts Bluff NM is far from the Black Hills, it supports pine woodlands that are also covered by this model. The mid-elevation forest model applies to Jewel Cave NM, Mount Rushmore NMEM, and portions of Devils Tower NM and Wind Cave NP. The upper elevation forest model applies to portions of Mount Rushmore NMEM and to small areas of aspen or birch stands in other Black Hills parks. These models were formed based on unpublished reports, published studies of fire history in the Black Hills and fire effects on dominant species, USGS-NPS vegetation mapping reports, and discussions with NGPN staff. Further development of each narrative is need.

In the Black Hills, ponderosa pine is the dominant tree species across most of the landscape. As in ponderosa pine forests throughout the western U.S., absence of frequent fires in the Black Hills has led to increased tree densities and higher probabilities of high-intensity fires that formerly occurred rarely on most low- to mid-elevation sites. With several decades of fire suppression, dense stands may form that would burn with high severity. In the grassland / forest transition zone, absence of fire has allowed extensive tree encroachment in former savannas and grasslands. In the foothills of the Black Hills, established trees may mature and be able to endure light and moderate intensity fires, leading to a savanna state that resists return to a pure grassland state.

However, the environment, disturbance characteristics, and biogeography of the Black Hills has created important differences in the structure and dynamics of these forests compared to ponderosa pine forests of the Southwest, eastern Cascades and Columbia Basin, and Rocky Mountains. Most precipitation in the Black Hills occurs during the growing season, creating excellent conditions for seed germination and establishment in moist years (Figure B-24; Boldt et al. 1983; Shepherd and Battaglia 2002; Brown 2006). During moist years, this allows rapid formation of dense regeneration near an existing seed source. (Dispersal distance of seed is ~ 76 m; Boldt et al. 1983.) In addition, although Black Hills pine forests were dominated by frequent low-intensity fires, the more mesic conditions of this region produced longer intervals between fires than in other ponderosa pine regions. The Black Hills climate included long periods of favorable years for pine establishment as well as long dry periods. As a result, the Black Hills may have had higher spatial and temporal variability in recruitment, stand structure, fire-return intervals, and fire intensity than other regions dominated by ponderosa pine (Brown 2006; Brown and Cook 2006). Unlike many regions where it is present, ponderosa pine is the only conifer tree species throughout much of the Black Hills. Succession to dominance by a more shade-tolerant species is possible only in moist, cool sites where spruce is present. Finally, in the Black Hills, dwarf mistletoe does not affect ponderosa pine, in contrast to most regions where this pathogen is an important disturbance agent (Boldt et al. 1983).

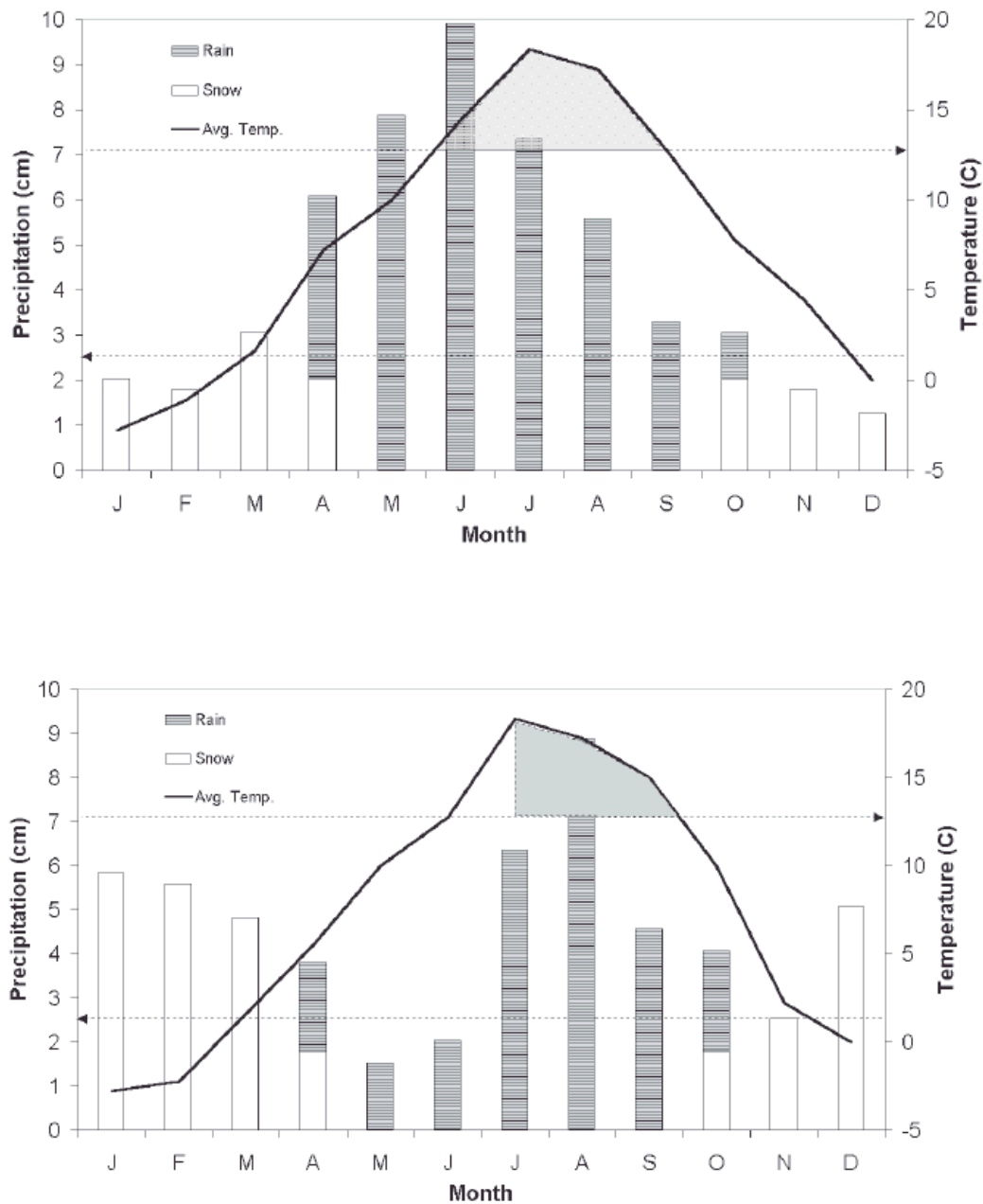


Figure B-24. Climatic differences in regions dominated by ponderosa pine.

Average monthly precipitation (bars) and temperature (line) in a) the Black Hills; b) the U.S. Southwest and Rocky Mountain regions. Dotted arrows indicate the minimum precipitation and temperature required for ponderosa pine seed germination. Shaded gray area between the average temperature line and the minimum germination temperature arrow indicates period in each region when conditions are optimal for seed germination. Source of figure and caption: Shepperd and Battaglia (2002: Figures 34 and 35).

Black Hills Ponderosa Pine Savanna and Forest / Grassland Transition (Figure B-25):

The savanna model applies primarily to the grassland/forest ecotones at Wind Cave NP and Devils Tower NM, but it is also relevant for pine and eastern red-cedar woodlands at Scotts Bluff NM. This model distinguishes states based on tree structural composition. However, transitions in the dominant characteristics of the grass stratum will also occur due to grazing, fire, succession, or precipitation. Particularly in open sites where the grass understory is well-developed, transitions covered by grassland models are also relevant here.

Transitions in this model are a function of fire frequency, grazing, and moisture availability. Prior to settlement, this area was a mosaic of grasslands, open woodlands and savanna dominated by grasses and large fire-resistant pines with small regeneration patches, and some denser woodlands, primarily on moister north slopes of steep canyons. Savannas were characterized by low-severity fires with an average return interval of 15-years. Except for deep ravines and steep north slopes of these canyons, most of Wind Cave NP and Devils Tower NM probably were characterized by frequent low severity late-summer fires (mean fire return interval of 10-14 yrs (Fisher et al. 1987; Brown and Sieg 1999). Mixed or moderate intensity fires occurred less frequently on sites or under conditions that allowed denser stands to form (~every 75 years on average), while high-severity fires were rare (~every 240 yrs.) In the last 150 yrs, absence of fire has allowed encroachment of pine into grassland areas, and increased density of pine turning savannas into denser woodlands and forests. In parts of the western U.S., this altered fire regime has been attributed to the effects of livestock grazing. In the Black Hills, it is unclear whether grazing was as important in reducing fire frequency (Bachelet et al. 2000), or whether active fire suppression combined with favorable conditions of the Black Hills climate for growing trees were sufficient.

Prior to fire suppression, transitions to a closed-canopy forest state occurred infrequently. Currently, this state is common but is unstable, with a high likelihood of being turned to an early seral state by stand-replacement high-intensity fires or insect outbreaks. After such hot fires, sites are characterized by bare ground and weedy species, with grasses and shrubs recovering and colonizing in a few years. The savanna model identifies major threshold transitions between grasslands and early seral states to either invaded or forested states. However, in these savanna areas, fire-driven transitions back across the threshold between forests and grasslands occur without high management inputs. If dense forests persist long enough in former grasslands, presumably the post-fire pathway might lead to a different community type than the original wheatgrass or bluestem community that was present before encroachment. Apart from this possibility, the most stable post-encroachment state probably is the open canopy, large tree state. In the grassland / forest transition zone, absence of fire has allowed extensive tree encroachment in former savannas and grasslands. In the foothills of the Black Hills, established trees may mature and be able to endure light and moderate intensity fires, leading to a savanna state that resists return to a pure grassland state. However, with fire suppression or prolonged moist conditions, this state will move to a closed-canopy state that is unstable in these hot, dry foothills.

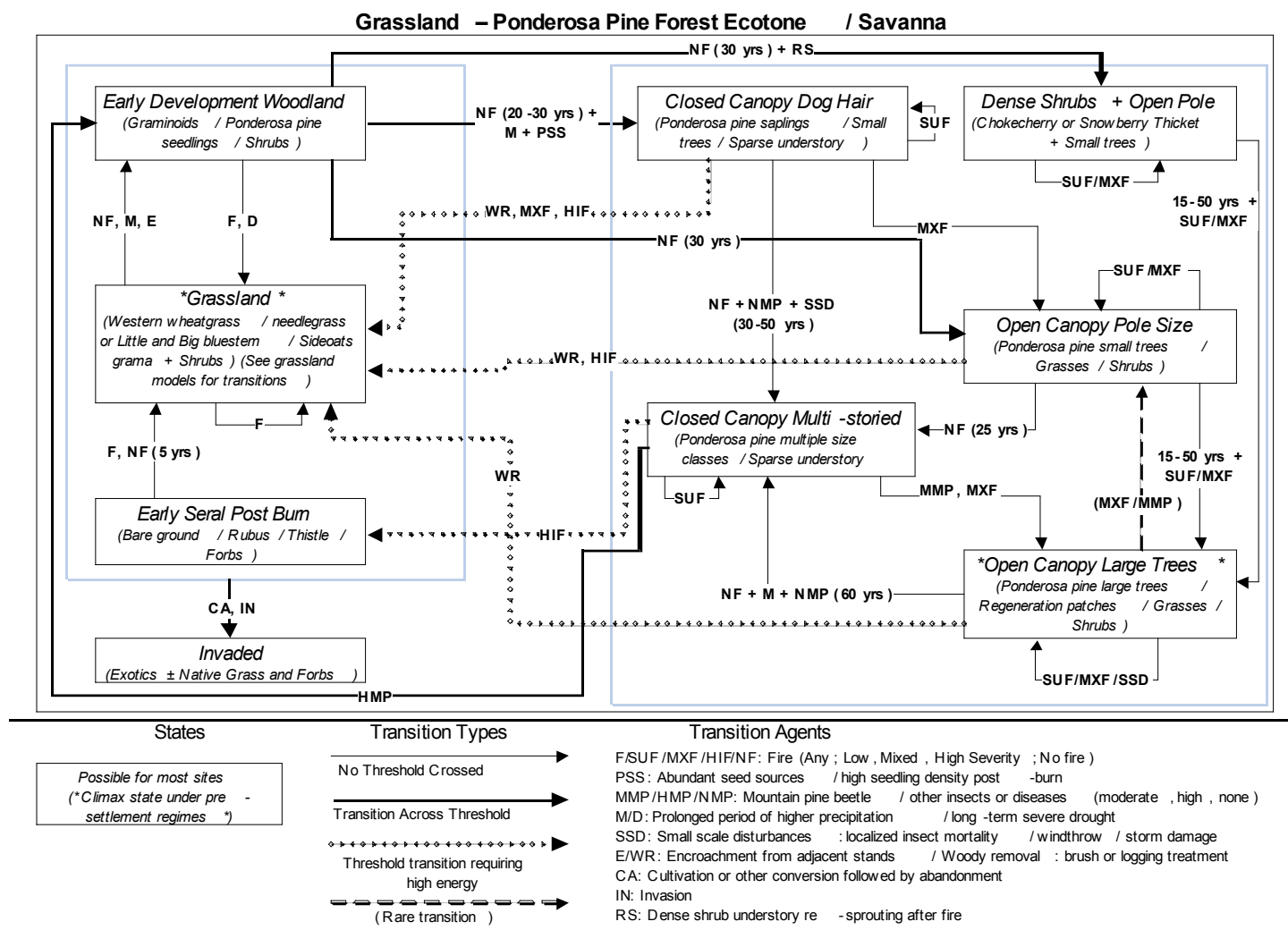


Figure B-25. State-transition model for Black Hills foothills woodlands and savannas.

Mid- and Upper-Elevation Ponderosa Pine Forests (Figure B-25):

Two models cover Black Hills forests in portions of the NGPN. The general mid-and upper elevation model covers Jewel Cave NM and drier portions of Mount Rushmore NMEM, which are in the interior south-central Black Hills. Portions of Wind Cave NP and Devils Tower NM fit into either this or the foothills model. A second model, covering higher, moister areas of Mount Rushmore NMEM and adjacent areas, incorporates hardwood birch/aspen forests as a more significant element; this model is summarized in the next section.

As in the foothills areas, low-severity fires probably were characteristic of areas covered by this model. Fire histories have been developed for NGPN parks in this site type. At Jewel Cave NM, low-severity fires ~16-32 yrs. predominated, although a fire-free interval of 79 years occurred before settlement (Brown and Sieg 1996). Fire ecologists have debated the relative of importance and scale of high-severity fires in the Black Hills. Shinneman and Baker (1997) argued that portions of the Black Hills may have been characterized by less frequent, stand-replacement events. Lentile et al. (2005) argued that the mixed-severity patterns of the Jasper fire suggest that the region had a more complex fire regime characterized by a mix of low, moderate, and high-intensity fires spatially and temporally over several centuries. Brown (2006) discusses these alternative theories, concluding that most of the landscape generally was characterized by frequent, low-severity fires producing relatively open forests. Brown (2006) concludes that patches of high-tree mortality were present but generally limited to small spatial scales, and that broader patches of stand-replacement events were rarely present across most of the landscape. Therefore, all ecological states present in our model likely were present historically. However, fire suppression has altered the dominant states from relatively open to denser closed-canopy stands, and continued stand-replacement fires, as have occurred in some portions of the Black Hills, may lead to much larger patches of early seral states following high-severity fires.

In both mid- and upper-elevation ponderosa pine forests of the Black Hills, including areas adjacent to Mount Rushmore NMEM, insect outbreaks have caused high mortality of mature trees. Given the high tree density at Mount Rushmore, NGPN managers and scientists are highly concerned that old-growth forests of this NMEM are at risk of severe mortality due to insects, high-severity fire, or both unless management treatments are implemented to reduce fuel loads and tree densities (Symstad and Bynum 2007). Two bark beetles that are most likely to attack trees in the Mount Rushmore area, and have a perceptible impact, are the mountain pine beetle (*Dendroctonus ponderosae*) and the pine engraver (*Ips pini*). Both of these insect species are endemic to the Black Hills and can exist within the forest as non-threatening populations; that is, they usually survive in limited numbers within weakened, stressed, or damaged ponderosa pines or, as is the case with pine engravers, they will also occupy wind-thrown trees and slash (Sheppard and Battaglia 2002). Generally, both beetles mentioned kill trees by feeding on the inner bark of ponderosa pines, while introducing a parasitic fungus that produces deleterious effects within the sapwood (Hagle et al. 2003). The combined effects of the beetle and the fungus can kill the tree within 1 year of the infection date (Christiansen et al. 1987).

Mountain pine beetles kill more trees in the Black Hills than any other insect (Allen 2003), and outbreaks occur every 11-20 years (Shepperd and Battaglia 2002). This species is prolific during an epidemic period, which can last up to 15 years (Allen 2003), and is responsible for tree mortality levels exceeding 25% (McCambridge et al. 1982, cited in Allen 2003). Pine engravers are less aggressive and survive mostly in damaged or downed trees and logging slash (Shepperd and Battaglia 2002). Consequently, trees that are scorched during fires can become prime targets for pine engravers, while outbreaks are typically less than 3 years in duration, and often occur over just a single season (Shepperd and Battaglia 2002). Additionally, when pine engravers attack live trees, the trees are often in the size class of 2-8" in diameter, at breast height (Shepperd and Battaglia 2002), or if larger trees are utilized, only the top of the tree may be attacked and killed by the beetles (Hagle et al. 2003). Meanwhile, the mountain pine beetles seem to prefer trees with diameters greater than 8" and may avoid the tops of trees because of the reduction in diameter and the thinning of the bark that occurs with height (Shepperd and Battaglia 2002). Dense ($\geq 120 \text{ ft}^2$ basal area per acre), even-aged stands, in the range of 7-13" diameter, appear to be the most vulnerable to mountain pine beetle attack (Allen 2003), while trees less than 5.0" in diameter are rarely attacked by this species (Hagle et al. 2003). In some instances, both bark beetle species may attack the very same trees, but they do so by exploiting different regions of the same bole (Shepperd and Battaglia 2002).

These insects can remain relatively unnoticed on the landscape for several years at a time. But, when environmental conditions are optimal (e.g., during droughty periods with warm winters, or following blow downs or fire [U.S. Forest Service 2000]), these same species may increase exponentially and also exploit a large number of healthy trees in the process. As a consequence, their activity becomes quite obvious as portions of the forest fade from green to red and brown and many trees are killed. Ecologically, however, bark beetles are considered a natural source of disturbance, and their presence within the forest promotes structural heterogeneity (Knight 1994, U.S. Forest Service 2000).

Still, there are concerns regarding bark beetle outbreaks: Stand susceptibility may be increasing due to drought and crowding, while the dieback of a large number of trees could have other repercussions. Temperatures are warming in the Northern Great Plains area (National Assessment and Synthesis Team 2000), and in conjunction with periodic droughts, forest soils within the Black Hills may become drier over time and more trees may become weakened from water stress. Also, with the advent of Anglo settlement and fire suppression, it is quite evident that the density of trees in the Black Hills has increased (Progulske 1974; Grafe and Horsted 2002), and stand crowding has been identified as an important variable contributing to bark beetle outbreaks (Sartwell and Stevens 1975, cited in Sheppard and Battaglia 2002). A recent forest inventory at Mount Rushmore National Memorial (MORU) reveals that the average live tree density is 382 ponderosa pines per acre (diameter breast height [DBH] > 1"), with an unusually high number of small diameter trees being present (i.e., trees 1"-8" DBH) (Symstad and Bynum 2007). In the event that large areas of beetle-killed pines are produced on the landscape, the likelihood of an intense wildland fire may increase from the accretion of fine fuels on the forest floor and heavy, seasoned fuels in the overstory.

Black Hills Mid - and Upper Elevation Ponderosa Pine Forests

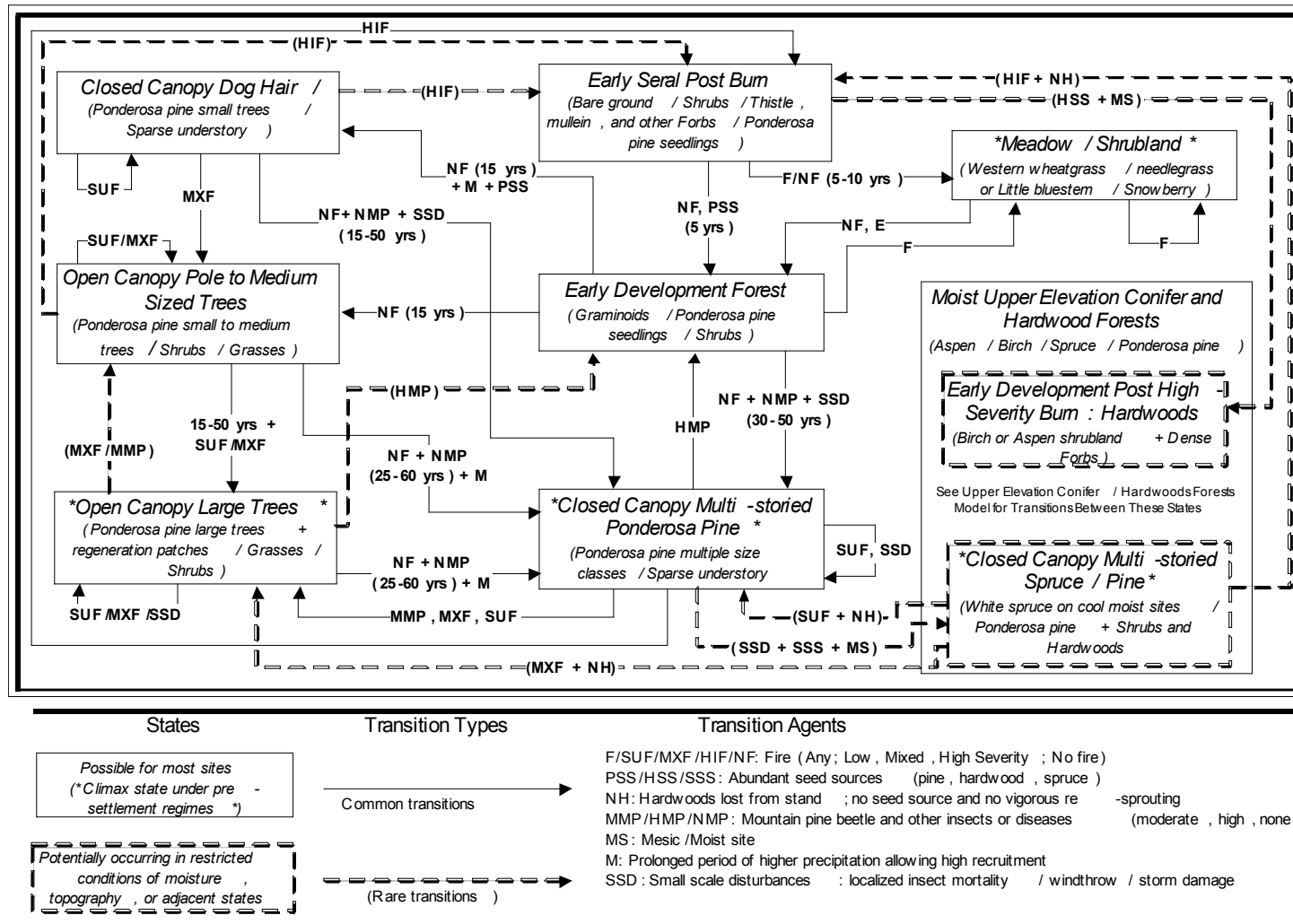


Figure B-26. State-transition model for Black Hills mid- and upper-elevation pine forests.

Mid- and Upper Elevation Conifer and Conifer/Hardwood Forests (Figure B-26):

A second Black Hills forest model covers higher elevation mesic sites in the Black Hills. At 4,000-7,000 ft in the Black Hills, patches of aspen (*P. tremuloides*) and paper birch (*Betula papyrifera*) often are present in draws and north slopes. These stands are more extensive in the northern Black Hills rather than in NGPN parks in the central Black Hills and foothills. Although aspen can dominate less-mesic sites than paper birch, both species often occur together and aspen/birch types may intergrade. White (“Black Hills”) spruce (*Picea glauca*) forms mixed stands with hardwoods or pine in this type, with some pure spruce stands found in cool drainages in the northern Black Hills. White spruce is common in cool, moist areas at higher elevations of the Black Hills; Mount Rushmore NMEM is at the lower edge of this spruce zone. Deciduous riparian forests of oak, ash, and boxelder in the Black Hills foothills are not included in this model.

Spruce and hardwood stands are minor elements or absent at most NGPN parks. Small aspen patches are present at Wind Cave, Devils Tower, and near Jewel Cave. Mount Rushmore supports small (<1-3 ha) aspen and birch stands. Only Jewel Cave has a mapped occurrence of an aspen-dominated type although aspen stands are present at Wind Cave NP. Spruce is a very minor element at Mount Rushmore. It is present mainly as a narrow riparian stringer of mature trees intermixed with pine in Starling Basin, and as an uncommon understory tree in cool sites.

Despite their minor contribution in terms of area, spruce and hardwood patches are important elements of habitat diversity in what otherwise is a natural monoculture of ponderosa pine. To some extent, the role of aspen and birch patches in Black Hills forests mirror the function and importance of hardwood draws in NGPN grassland parks. As in coniferous forests of the Rocky Mountains, aspen patches are heavily used by wildlife such as elk and cavity-nesting birds. For example, aspen stands support higher songbird diversity than ponderosa pine stands, and several species may not occur in the absence of aspen stands (Rumble et al. 2001; Mills et al. 2000). Aspen stands are of management concern at Wind Cave, where an exclosure and prescribed fire has been used to stimulate and protect aspen regeneration. Adjacent to Mount Rushmore in the BHNF, spruce and birch are present in larger stands, and their occurrence at the park could change depending on fire occurrence or climate variation.

This model applies to mesic sites that support aspen or birch as distinct patches or as small clumps in conifer forests, generally in draws and drainages, cool lower slopes, and north slopes. Dominant agents determining transitions are fire, browsing intensity, availability of seed sources or resprouting hardwoods, and successional changes. When hardwoods are present, mixed- to high-intensity fires lead to rapid resprouting or regeneration by seed from surviving stems. On drier sites, hardwoods might not be present to regeneration if suppressed by continued heavy browsing or removed by several fires within a few years. In these rare situations, transition to a meadow state and then to a pine-dominated pathway is possible. The boundary between hardwood and pine stands is likely to be dynamic, and mixed- or high-intensity disturbances in these sites probably include all types of transitions (hardwood to hardwood, hardwood to pine, pine to hardwood, pine to pine).

Usually, hardwoods will dominate the site in a shrubby, small tree, and then large-tree states. With heavy browsing by deer or elk, the early seral state may persist as a shrubland until browsing is reduced. In the mature hardwood condition, small disturbances may allow some aspen regeneration; with light to moderate browsing, no conifer encroachment, and low-intensity disturbances, the mature aspen state may persist. With heavy browsing, lack of regenerating hardwoods leads to an open stand if conifers do not colonize the site. In the Black Hills parks, more typically spruce and pine seedlings would be established either soon after stand initiation or when the canopy opens in the mature hardwood state. Without fire, conifer regeneration will grow from sapling to sub-canopy to canopy-dominant positions. As mature trees, ponderosa pine will persist through surface and mixed-intensity fires, which will stimulate patches of hardwood sprouting.

Fire kills spruce except for some mature trees in very light surface fires. In other regions, a single fire may kill most spruce but seed from trees killed in moderate intensity autumn fires can germinate on mineral soil and form dense spruce stands. This pathway is unlikely in the Black Hills (except in small patches) due to the prevalence and fire tolerance of ponderosa pine. However, stands dominated by spruce, with a few residual pine, could result from long periods (200 yrs, speculatively) without disturbance in mesic sites, due to the intermediate shade tolerance of this species. Mountain pine beetles could speed up this successional pathway by removing most large pines without killing most spruce. In contrast, repeated broad-scale fires (multiple fires $\sim < 40$ yrs; Nienstaedt and Zasada 1990) will eliminate most of the existing seed source. In the Black Hills, we speculate that moisture and temperature availability limits spruce to moderate or moist sites, and that historically, frequent fires in moderate sites further restricted spruce to moister sites characterized by a mixed-intensity fire regime. Therefore, with continued fire suppression, spruce is becoming slightly more widespread in the Black Hills than it was historically. At Mount Rushmore, this “expansion” limited to a few spruce saplings in uplands adjacent to the very small portion of the park supporting mature spruce (R.A. Gitzen, pers. obs.). Presumably, climate changes resulting in hotter, drier summers could restrict the range of spruce further in the Black Hills, potentially excluding it from Mount Rushmore. However, more review of environmental limitations to spruce regeneration vs. projected climate changes is needed to determine if this loss is plausible.

Black Hills Mid - and Upper Elevation Hardwood / Conifer Forests

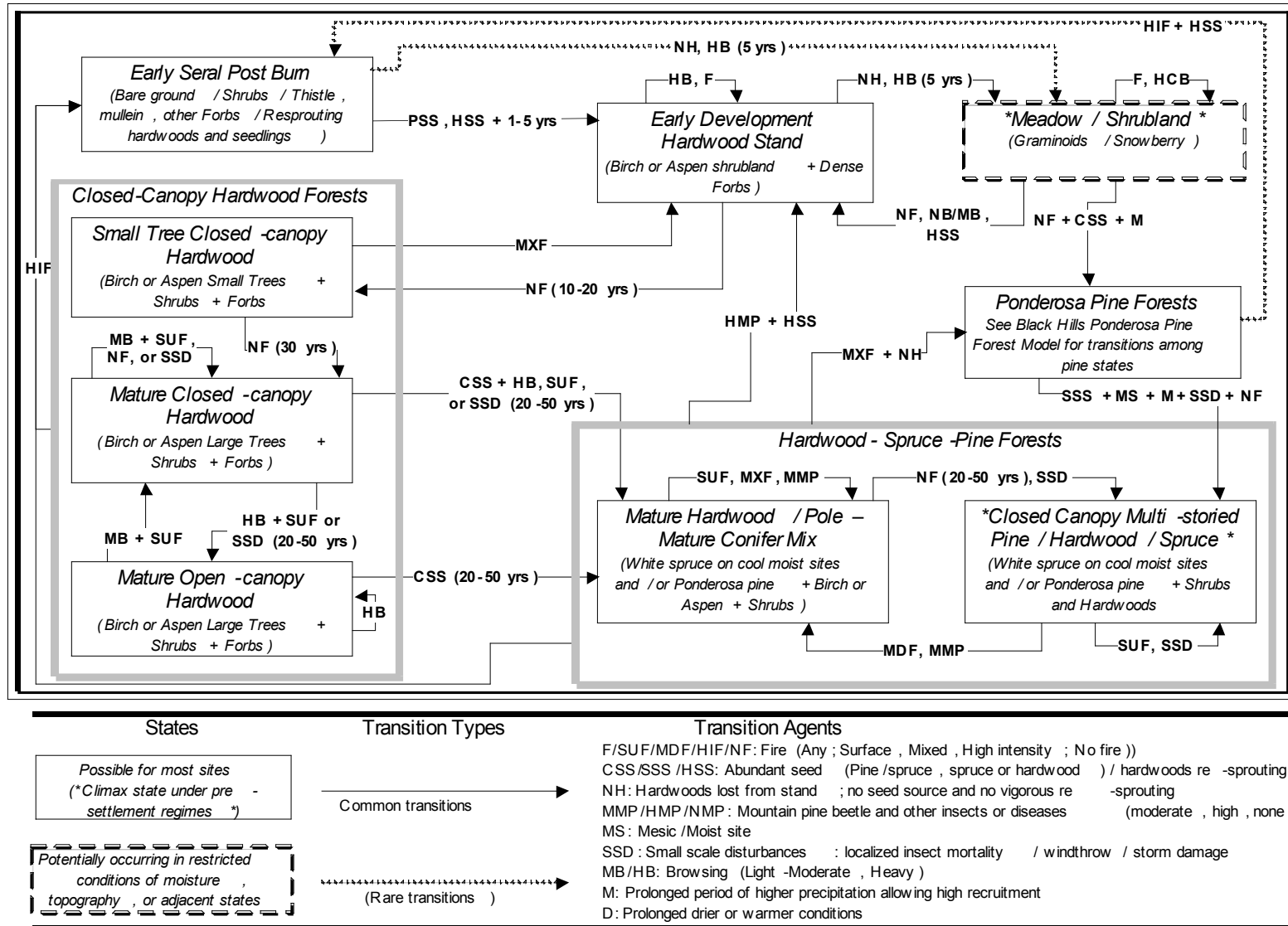


Figure B-27. State-transition model for Black Hills mid- and upper-elevation conifer/hardwood forests.

Upland Oak Communities (not modeled):

Upland woodlands dominated by bur oak are present in the northern Black Hills. Transitions between pine and oak savannas and woodlands could occur in foothills areas, and transition between oak and pine forests could occur in mid-elevation areas oak stands or pine stands with oak understory. Other than in small patches, bur oak is a very minor component of upland sites of Wind Cave and Jewel Cave. Transitions to an oak-savanna state were assumed to be unlikely or not relevant in the Foothills model. Oak and pine-oak dominated types are present outside of Mt. Rushmore. At Devils Tower NM, a ponderosa pine / bur oak type is present in draws, and oak is present in the understory of many pine-dominated sites. In these areas, bur oak may resprout and dominate the community if a stand-replacement fire kills the pine overstory. In patches dominated by oaks currently, fire of any severity would remove encroaching conifers; small oaks would resprout while large oaks could survive light to moderate fires. However, there are few patches in NGP parks where oaks are abundant enough such that resprouting oaks could dominate the new stand after fires.

Lessons learned, hypotheses formed, and questions raised by model development

As in the rest of the Great Plains, fire, grazing, and precipitation play critical roles in structuring vegetation communities in the NGPN. In addition, the individual and interacting effects of landform, hydrologic processes, and soil type shape the landscape composition of cover types. Differences in soil type and topography partially determine whether a grassland fits into western wheatgrass, needleandthread/grama, little bluestem, or sandy-site types. Erosion and landform produce extensive badlands features and suitable sites for critical woody habitats in a predominately grassland region. When floodplains no longer are flooded because of dams or shifts in river channels, cottonwood forests succeed into shrublands and grasslands.

Compared to many systems, NGPN systems have faced minor risks of threshold changes caused by weather fluctuations, heavy grazing, and high disturbance. The state-transition/non-equilibrium framework was developed in regions such as the U.S. Southwest and sagebrush steppe. In contrast to these systems, upland areas of the NGPN have faced little risk of undergoing major transitions across thresholds to stable degraded states. For example, during the 20th century, some grasslands of this region rapidly recovered rapidly after cessation of prolonged heavy cattle grazing and drought, moving from shortgrass-dominated states to mixed-height grasses.

However, invasive species are now widespread. Exotics and climate change may lead to high likelihood of undesired threshold changes that formerly were not relevant. For example, on some sites, interactions of drought, bison grazing, and prairie dogs produces sparsely vegetated areas, with high cover of bare soils. Although such sites may have recovered quickly in the past if prairie dogs were removed, now there is a risk that bindweed and other exotics could dominate these sites (A. Symstad, USGS, pers.

comm.). Exotics and climate change. Alternatively, some exotics might dominate sites only as part of a transitory early successional community. We need further thought and work to understand where and under what conditions “new” alternative degraded states may form in the NGPN.

Unlike many grasslands and arid areas of North America, neither extensive loss of shrubs or conversion of grassland sites to shrublands has been a major degrading factor in the NGPN. In many parts of western North America, exotic annual grasses (particularly cheatgrass) change the system dramatically, particularly by providing fuels to support more frequent fires. In the NGPN, annual grasses can invade and dominate many sites. However, except in draws, riparian areas, badlands topography, or the Black Hills, most sites in this region supported near-continuous grass cover sufficient to carry frequent ground fires. Therefore, annual grasses probably have little effect on fire regimes or on persistence of shrublands, although this does not imply that annual grasses will have minor effects on nutrient and water flow and native diversity.

Conversely, in most of the NGPN away from the Black Hills, fire suppression and reduction of river flows have not lead to rapid expansion of woodlands or shrublands. Rather, degradation and loss of riparian woodlands (see below) and green ash draws is of much higher concern. This is in contrast to expansion of eastern-red cedar east and south of most NGPN parks (but affecting areas near Missouri NRR and Niobrara NSR), expansion of riparian woodlands along the Platte and other rivers south and west of our region and undesired transitions to shrubland states in arid systems in the Southwest and Colorado Plateau. In grasslands of the NGPN, moisture availability and competition with grasses interact with fire, restricting woody communities to sheltered, mesic sites. We need more detailed examination of whether woody expansion will be a bigger threat due to climate changes, increased atmospheric carbon, invasion, and range expansion by eastern red-cedar.

Of the native communities in the NGPN, floodplain forests are most likely to be lost or permanently altered over much of the region under status quo climatic conditions. Some healthy riparian forests are present in the NGPN. However, in some parks and most of the landscape, changes in flood and flow regimes have turned many former floodplain woodlands into sparse cottonwood stands with old, dying trees and no tree regeneration. Along most dammed reaches, this critical habitat for woodland birds and other species is disappearing. Because of lowered water tables and absence of floods, the sites may not be restorable through large-scale planting efforts. In other cases, cottonwood regeneration may be absent but green ash and other deciduous trees may continue to provide woodland habitats; whether their continued existence is threatened by ungulate browsing of regenerating saplings needs to be quantified.

Black Hills forests and savannas face the typical problems caused by fire suppression in dry forest types across North America: encroachment into neighboring grasslands, and development of high tree densities and fuel loads in closed-canopy forests. Because of abundant growing season moisture during some years, these problems develop even faster in the Black Hills than in other regions dominated by ponderosa pine.

Changes in seasonality of precipitation in the NGPN, as in other region, may be or more important than precipitation amount in driving transitions between grassland and woody dominated states. Abundant summer precipitation in many years supports rapid establishment of ponderosa pine in the Black Hills, and may favor grasslands vs. the sagebrush-dominated states more widespread to the west of this region. As in other regions, changes in mean precipitation and temperature may have lower impacts than changes in precipitation timing (Suttle et al. 2007) and frequency of extreme events (Jentsch et al. 2007). With further work and discussion among relevant experts, these initial state-transition models can help form the basis for hypotheses about the effects of such changes on NGPN ecosystems, and help us to identify site types, monitoring measures, and analytical methods for attempting to detect major changes to these ecosystems before the changes are irreversible.

Exotic (Invasive Nonnative) Plant Species and Early Detection in the NGPN

The rationale for monitoring exotic plant species is straightforward: exotic plant species are known to alter the composition, structure, and function of natural ecosystems (i.e., impair biological integrity); and therefore, there are legal mandates and official policies regarding the management of such species on park unit lands and within park unit waterways.

The introduction of nonnative plant species into natural areas can rapidly change the habitat and lead to the displacement of indigenous species through superior competition for space and resources. In the Northern Great Plains exotic plants are exploiting new habitats, displacing indigenous species, and modifying ecosystems and natural processes. Some well documented invasions into the prairies, hills, and drainages of this area are linked to such introduced species as cheatgrass (*Bromus tectorum* L.), leafy spurge (*Euphorbia esula* L.), Canada thistle (*Cirsium arvense* [L.]), purple loosestrife (e.g., *Lythrum salicaria* L.), saltcedar (e.g., *Tamarix ramosissima* Ledeb.), and Russian olive (*Elaeagnus angustifolia* L.). In such cases, community composition and species abundance are immediately subject to change in host ecosystems, while biodiversity may ultimately be placed at risk within ecosystems located in the NGPN. For example, purple loosestrife occurs in monotypic stands along the Niobrara and Missouri Rivers at Niobrara National Scenic River and the Missouri National Recreational River, respectively, where this wetland invader has choked out other native plant species on 4,940 hectares (2000 acres), and is impinging upon the critical habitat of the piping plover (*Charadrius melodus* Townsend, 1837) (NPS 2005a). Canada thistle is another exotic species capable of creating monocultures, diminishing plant species richness, and reducing wildlife habitat quality (Krueger-Mangold et al. 2002). Between 2002 and 2006, the Exotic Plant Management Team (EPMT) documented, on average, over 1500 Canada thistle infestations/year across the NGPN park units (NPS 2006), where this species is often located in grassland settings, riparian zones, and within disturbed forest understories (e.g., on treefall mounds or sites that have recently been burned or thinned).

Similarly, the presence of leafy spurge in the Little Missouri River Basin has negatively impacted native plant communities. At Theodore Roosevelt National Park (THRO), Butler and Cogan (2004) found that leafy spurge had reduced plant species richness by an average of 61% within 10 plant associations, and at least 30 native species, occurring in all of the non-infested control stands, were competitively excluded from the infested sites. Findings from a previous study at THRO (Trammel and Butler 1995) indicated that the biomass of forage species, and therefore habitat use by deer, elk, and bison, was often diminished in plant communities infested with leafy spurge.

Natural ecosystem processes on the Northern Great Plains can also be affected by nonnative species. For instance, when cheatgrass invades arid or droughty native prairies, the damaging effects of fire can be enhanced (Grace et al. 2001), while in open

coniferous forests, this species contributes to the likelihood and magnitude of fire (Stewart and Hull 1949; Harrod and Reichard 2001). In other words, cheatgrass can alter the disturbance regime in grassland and forest ecosystems by increasing flammability, ground fuel continuity, and fire frequency (Brooks et al. 2004). Another introduced grass species, *Agropyron cristatum* (L.) Gaertn., has been shown to alter nutrient cycling, carbon sequestration, and succession on native prairies (Christian and Wilson 1999; Bakker and Wilson 2004). In such case, nitrogen and carbon storage in soils under crested wheatgrass are lower than in native grasslands, and colonization by native grasses is thwarted by the presence of this exotic species.

In riparian corridors, Russian olive and saltcedar appear to have a competitive advantage over native cottonwoods and willows (Shafroth, Auble, and Scott 1995; Shafroth et al. 2005), especially where the flood regime has been altered by human activities (Katz and Shafroth 2003; Stromberg et al. 2007). Because Russian olive is shade-tolerant and associated with nitrogen-fixing bacteria, unlike cottonwoods, riparian plant succession and nutrient cycling are two ecosystem processes likely to be affected by the presence of this species (Katz and Shafroth 2003). Even where stream flow remains unregulated, saltcedar can colonize riparian areas and change flood plain development via encroachment and the subsequent narrowing of stream channels (Birken and Cooper 2006), while numerous other studies indicate that wildlife taxa (e.g., breeding birds) favor cottonwood and willow habitats over the shrublands dominated by saltcedar (see Shafroth et al. 2005). Additionally, saltcedar stands now occur on more than 470,000 ha (1,000,000+ acres) in the western U.S., where they utilize streambed aquifers to a greater extent than their native counterparts by penetrating deeper into the substrate and extending farther from the stream bank (Zavaleta 2000). In other words, stream flow, sediment deposition, wildlife habitat quality, and plant water use in riparian areas can be affected by the presence of saltcedar anywhere this species occurs within the western United States and northern Mexico.

Clearly then, introduced plant species can have a significant ecological impact when they are released, accidentally or purposely, outside of their native range, and the economic costs to eradicate or control the plants can be substantial once they are established. To keep newly invading species from further degrading NGPN ecosystems, early detection is essential, so that these species can be controlled or eliminated before multiple populations are established and spreading rapidly (Figure B-28). However, detecting small populations is akin to looking for a needle in a haystack, posing major challenges for development of an early detection protocol.

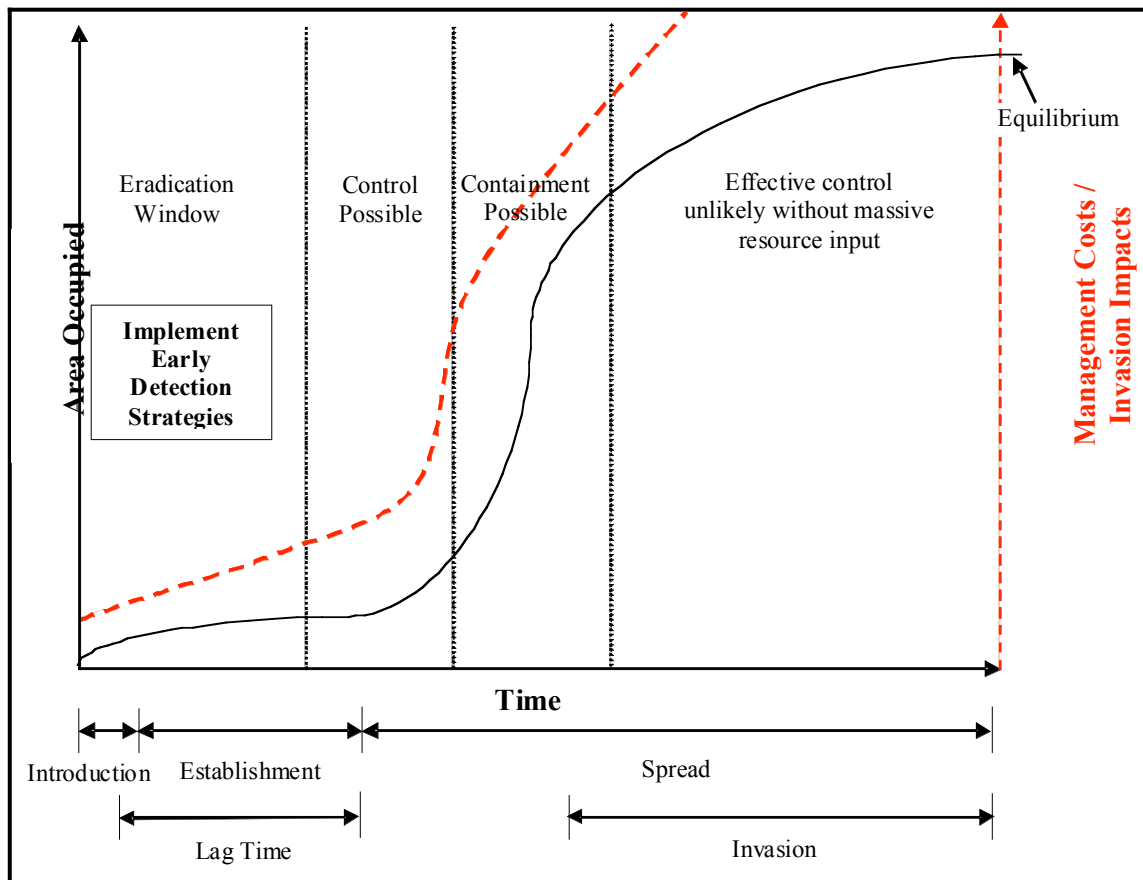


Figure B-28. Biological stages of invasion vs. management costs and invasion impacts. Appropriate management strategies are shown to illustrate the relevance of the invasion process to management options. As invasive species become more entrenched, the costs of managing them become significantly greater, to the point of being cost-prohibitive. *Eradication* = total elimination of all plants and associated plant material, *control* = partial elimination of new and existing invasive plants and associated material, and *containment* = limiting the spread of invasive plants to existing populations (from Welch 2007; after Chippendale 1991, Naylor 2000, and McNeely 2001).

Terrestrial Ecosystem Models: Vertebrate Dynamics

Prairie Dogs in NGPN Mixed-grass Ecosystems

The black-tailed prairie dog (*Cynomys ludovicianus*) once ranged the Great Plains from the Canadian province of Saskatchewan to northern Mexico (Johnsgard 2005). Five species of prairie dogs can be found in North America; the black-tailed, Mexican, (*C. mexicanus*), white-tailed (*C. leucurus*), Gunnison's (*C. gunnisoni*), and Utah prairie dog (*C. parvidens*) (Johnsgard 2005). The black-tailed prairie dog is the most abundant of the five sub-species, is native to the Northern Great Plains (Cincotta et al. 1988) and can be found in five National Park Service Units in the NGPN.

Early settlers and French explorers named the animals “petits chiens,” or little dogs (Johnsgard 2005). During their journey up the Missouri River, Lewis and Clark noted that “wild dogs of the prairie” appear in seemingly infinite numbers. Naturalist Ernest Thompson Seton estimated that approximately 5 billion prairie dogs inhabited North America in the early 1900's (Hoogland 2006). During the 20th century, however, conflicts between prairie dogs and land-use interests have escalated, resulting in widespread reduction of prairie dog colonies and numbers through habitat loss, fragmentation and control efforts (Foster and Hygnstrom 1990). Some authorities estimate that the black-tailed prairie dog now only occupies approximately 2% of its historic range (Miller et al. 2007).

Prairie dogs are members of the Sciuridae or squirrel family and are closely related to ground squirrels, chipmunks, woodchucks and marmots. They are small, short-tailed animals with eyes and small ears set far back on their heads. Their light brown fur usually blends well with the surrounding soil and dome mounds created by their digging and burrowing. Named for their bark like warning calls and black-tipped tail, black-tailed prairie dogs average 14 to 17 inches in length and generally weigh between one and three pounds. With their short, muscular legs and long-nailed toes on both front and hind feet, the animals are well equipped for their burrowing lifestyle (Hoogland 1995).

Prairie dogs live in colonies or towns that generally consist of varying numbers of closely spaced burrows, some of which can exhibit elaborate networks of interconnecting tunnels, cavities, and multiple entrance holes that provide escape routes from pursuing predators and from flooding (Hoogland 1995). Typically, prairie dog colonies can have 30 to 50 burrow entrances per acre but not all of the entrances will be characterized by a dome mound that is created by stock piling and packing soil around the burrow entrance (Hoogland 1995). These dome mounds can reach two feet in height and ten feet in diameter. The mounds serve as lookout stations and can prevent water from entering the tunnels. Each burrow entrance usually leads to a tunnel that can be from three to six feet in depth and extend as much as 15 feet in length (Foster and Hygnstrom 1990). The size and complexity of each burrow system varies greatly. The animals will frequently

excavate one or more small chambers just below the surface, where they can retreat to safety, sit and listen for above ground activity. Deeper underground, they dig nest chambers where they can rest, sleep, and raise young with a greater degree of security.

Prairie dogs are very social animals, living in towns that range in size from 3-5 acres all the way up to 1,000 acres or more in some localities (Johnson and Collinge 2004; Foster and Hygnstrom 1990). The average prairie dog colony size in NGPN park units is approximately 40 acres (J. Wrede, NGPN, unpublished data.). Some large colonies can be divided into wards by barriers such as ridges, lines of trees or shrubs, roads, canals and other physical features that generally restrict movements. Prairie dog colony expansion or growth is heavily influenced by the presence of tall vegetation and/or vertical barriers (Figure B-29). Animals in one ward may be able to see and hear those of adjacent wards, but movement between the wards is usually highly limited. Within a ward, each family group or “coterie” of prairie dogs occupies a territory of approximately one acre. A coterie usually consists of a single adult male, one to four adult females and any of their off spring less than two years old. All animals within the coterie and particularly the dominant male will vigorously defend their territory within the colony (Hoogland 1995).

Black-tailed prairie dogs reach sexual maturity after their second winter and breed only once per year. In the southern part of their range, they may breed as early as January while in more northern climates the breeding season does not generally begin until March. The gestation period for prairie dogs is 34 to 35 days and litter sizes range from one to six pups. The young are born naked, blind and helpless and remain underground for the first six weeks of their lives (Hoogland, 2006; Johnsgard 2005). The pups emerge from their dens during May and June and are normally weaned shortly thereafter. By the end of their first fall, the pups are nearly full grown and it is difficult to distinguish them from the adults in the coterie. Survival of prairie dog pups is high when compared to other animals, in part, because they spend so much time underground. Pups are also alerted to predation by the numerous sentries that maintain vigilance over the colony.

Female prairie dogs usually spend their entire lives in their original coterie, but young males move away in late spring/early summer before their first breeding season (Foster and Hygnstrom 1990). Some move to neighboring coterie, while others may travel as much as five miles or more before establishing territories in other colonies. Dispersal and pioneering is a risky undertaking for young prairie dogs and high mortality rates generally occur when the animals leave the safety and security of their coterie and burrow systems.

Female prairie dogs can live to an age of eight years while normal life expectancy for males is five years or less (Hoogland 2006). Even with sentries and their underground lifestyle, predation is the primary natural cause of mortality in prairie dogs. Badgers are a significant predator in a prairie dog colony because they have the ability to literally dig a

prairie dog out of his burrow. Weasels and the black footed ferrets easily follow prairie dogs throughout their burrows capturing them for an easy meal (Foster and Hygnstrom 1990). Other predators such as coyotes, bobcats, swift fox, hawks and eagles are regular visitors to prairie dog colonies (Agnew et al. 1987).

Prairie dogs are highly susceptible to several diseases, the most notable being sylvatic plague, a severe infectious disease caused by the bacterium *Yersinia pestis*. The plague bacteria has proven to be devastating in prairie dogs and other rodents, often leading to rapid decline and even complete disappearance of entire populations (Webb et al 2006). The *Yersinia* bacteria are most often transmitted by fleas which are common external parasites of prairie dogs and other Great Plains mammals. Other natural mortality factors affecting prairie dogs include accidents, starvation, weather, parasites and other diseases but anthropogenic activities have and continue to cause the greatest losses (Foster and Hygnstrom 1990). The conversion of native prairie to crop production has destroyed much of the original grassland habitat that was once occupied by prairie dogs (Hoogland 2006). Control measures implemented by private and public entities since the turn of the century are believed to represent the greatest cause of the widespread loss of the black-tailed prairie dog from the landscape in the NGPN (Foster and Hygnstrom 1990).

Prairie dogs and their colonies not only provide a food base for native predators but also establish or greatly influence both micro and macro-habitats that sustain numerous other species of insects, reptiles, amphibians, small mammals and birds (Agnew et al. 1987; Miller et al. 2000). Some of these species, such as the endangered black footed ferret, are completely dependent upon the prairie dog for its life requirements. Other species such as the mountain plover, maintain a facultative relationship within the colony habitat and adjoining landscape (Agnew 1983). Uresk and Hansen (1987) noted twice as many small mammal species utilizing their prairie dog colony study area than was found on adjacent mixed grasslands. Five studies stretching over the time period 1958 through 1983 documented 163 different species associated with the prairie dog ecosystem (Koford 1958; Agnew 1983).

Prairie dog colonies can be found on a wide variety of soil types and geographic distributions but there are some soil types, slope and hydrologic characteristics that prevent or severely limit the animal's ability to establish and perpetuate a colony over the long term (Bangert and Slobodchikoff 2000). Generally speaking, the animals prefer silt, silt loam, clay, clay loam, sandy clay or silt clay soils in an open grassland environment with sparse distribution of trees or shrubs. Optimum habitat patch size ranges between 2-3 hectares with less than 75% herbaceous cover (Cincotta et al. 1988). Prairie dogs will avoid sodic or poorly drained soils with a flooding frequency of less than 10 years (Cincotta et al. 1988). Poorly suited sites for prairie dog colony establishment include sand and very rocky soils in savanna or forested environments with vegetative heights exceeding 40 cm. Hydrologic characteristics in poorly suited habitat are represented by permanently saturated or sub-irrigated soils and range sites that experience flooding every five years or less (Hoogland 2006).

Prairie dogs spend most of their time above ground foraging. During the growing season, adult prairie dogs consume, on average, approximately two pounds of grasses and forb plants per week. Grasses tend to be preferred and comprise up to 95 % of the animals daily diet. Forb plants (broad-leaf, non-woody plants) become important in the fall when grasses begin to cure and broad leaves remain green. Prairie dogs also eat seeds and insects when available (Foster and Hygnstrom 1990).

Plant species composition within well established prairie dog colonies is generally comprised of native species in early seral stages. The ability to survive within prairie dog colonies usually depends upon the response of a plant species to grazing, anthropogenic stressors, prairie dog and other wildlife activities (Cincotta et al. 1989). In the short-midgrass ecosystem, persistent burrowing and feeding by prairie dogs can, over time, change the number and type of plants growing in the colony and keep that vegetation in the early seral stage (Cincotta et al. 1989). Grasses generally evident on prairie dog colonies are more characteristic of shortgrass prairie because of the reduced competition from the taller mid-grass species that are routinely grazed by ungulates or clipped by prairie dogs in order for them to maintain visual security in the colony (Deisch et al. 1990). With the reduction in competition from taller grasses, many other plant species, particularly forbs and other broad leaves, can become established.

Increases in forbs and at times, invasive plants, occur due to the repetitive digging and scratching of the prairie dogs that disturbs the soil surface and creates more suitable conditions for new plant establishment. Annual grasses such as downy and Japanese brome have encroached on some prairie dog colonies in the NGPN in spite of prairie dog clipping and foraging that normally causes plant death prior to seed maturation ((Foster and Hygnstrom 1990; J. Wrede, NGPN, pers. obs.). Perennial grasses are not impacted in the same manner since those species rely upon root systems to produce new plants. While it appears that long term use of a site by prairie dogs tends to promote buffalo grass and blue grass communities, rainfall and soil site characteristics have an important effect on plant diversity and density that occur annually on a prairie dog colony. Ungulate grazing is a major influence in the prairie dog ecosystem because the removal of standing forage on the perimeters of the colony provides improved conditions for colony expansion due to increases in visual security for dispersing animals (Cappock et al. 1983; Knowles 1986). Prairie dogs maintain vegetation at a higher nutritional level by continuously promoting new growth and thus, provide improvements in nutrition for grazing animals.

In recent years, prairie dogs have been recognized as a keystone species; in other words, a species that affects its primary ecosystem in a unique, significant and disproportionately large manner relative to its abundance (Kotliar et al. 1999; Bangert and Slobodchikoff 2000). It is clear that the animals influence grassland ecosystems through three vectors consisting of grazing, burrowing and as a primary prey species (Lomolino and Smith

2004). In addition, numerous species use colony sites for food, shelter, nesting and security, either facultatively or as habitat obligates. Black-footed ferrets, mountain plovers, burrowing owls, and at least 6 other species are entirely or mostly dependent upon prairie dogs and their colony areas for their survival, reproduction and other life requirements. At least 20 species receive routine, opportunistic benefits from colonies and over 117 species have natural histories in association with prairie dog colonies. Beside the list of identified vertebrates, other organisms such as protozoan's, arachnids, insects and 4 plant species are directly associated with the prairie dog ecosystem (Hoogland 2006). The burrowing activity of prairie dogs mixes subsoil and topsoil, redistributes soil nutrients and minerals, and promotes moisture retention and penetration. The combination of burrowing, foraging, and clipping alters vegetative composition and can affect the concentration of nitrogen in the soil and nitrogen uptake by plants. Even though prairie dogs reduce vegetation biomass, particularly at young colony sites, vegetation digestibility, protein content and productivity of both forbs and graminoid species is often enhanced (Hoogland 2006).

The prairie dog's influence on plant and animal communities in Northern Great Plains parks is substantial, unique and disproportionately large in comparison to its abundance on the landscape. Given that so many species are either dependent upon or directly associated with prairie dog colonies, it is reasonable to conclude that the black-tailed prairie dog can be legitimately classified as a keystone species and is critically necessary to maintain the integrity of grassland ecosystems (Kotliar 2000). In addition, the species can also be regarded as a foundation species due to the ecological functions it performs in proportion to its relative abundance (Hoogland 2006).

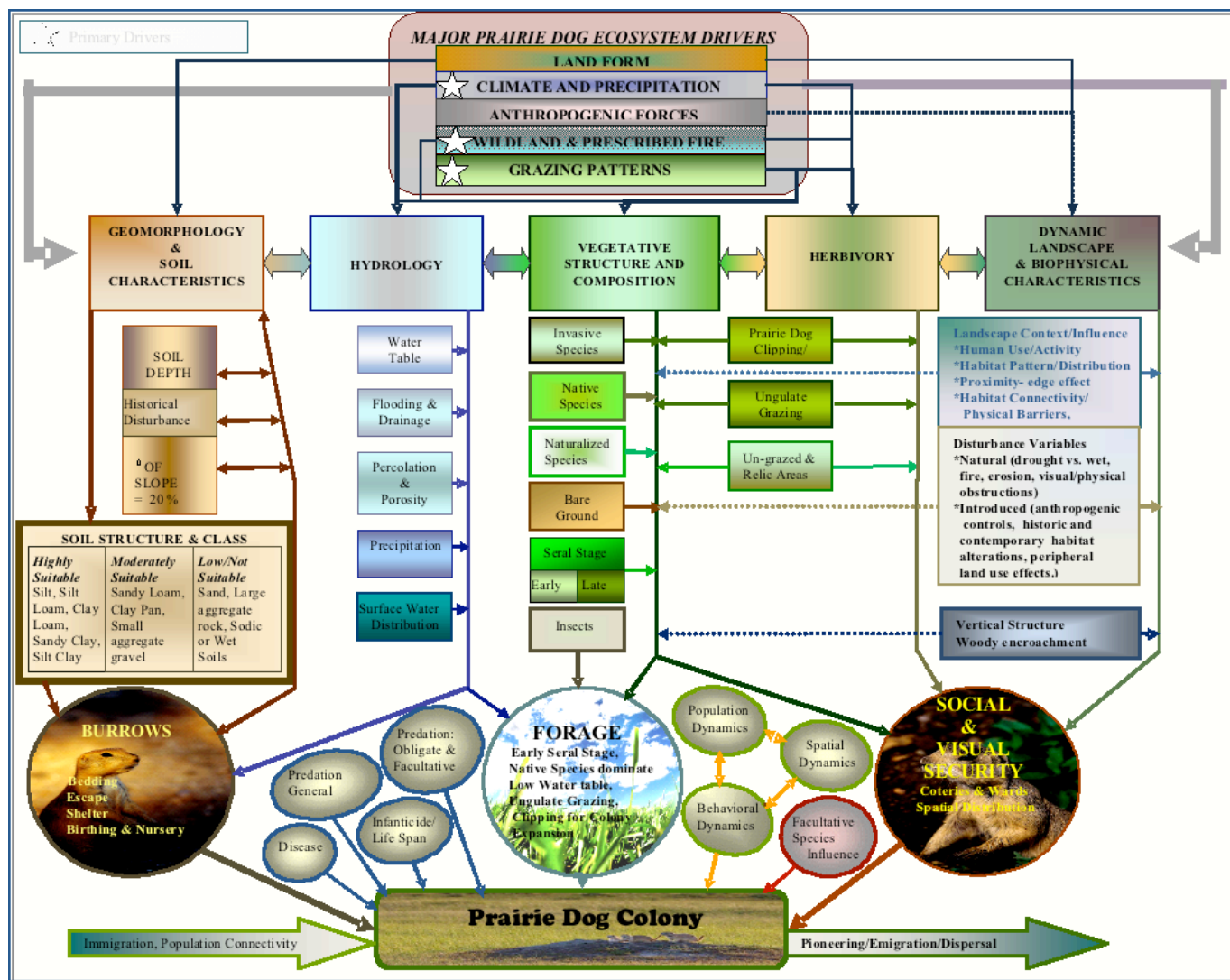


Figure B-29. Major factors affecting prairie dog occurrence and spatial distribution in the NGPN.

Interactions of Bison with Other Wildlife

According to NPS policies, all ecosystems in the Network are degraded since all are missing native organisms. When a species is missing, or their demographics or functions severely altered from natural conditions, there is often a ripple effect throughout a system. The absence of some species may have a disproportionately large effect on a system.

Bison are one such species that has been lost from all NGPN parks except the three largest parks (Badlands, Theodore Roosevelt, and Wind Cave NPs). This species characterized the Great Plains prior to its eradication from much of the. Bison were selected as the focal point of a faunal model (Figure B-30) because 1) they play a significant role in grassland ecology, 2) they are currently present and a significant management issue in three Network parks, 3) their absence affects ecosystem functioning in the other parks, and 4) they are a symbol of the region and the Network. Similar models could be developed for many other plant and wildlife resources. For purposes of simplification and clarity the model mostly omits direct effects on vegetation (however, see the other models) and focuses on bison interactions, directly and indirectly, with other grassland vertebrates. This model focuses on ecological effects of bison and predators on other vertebrates. Additional bison-driven processes are not addressed, such as nutrient cycling through grazing, trampling, and waste products, the creation of micro-heterogeneity in the landscape via wallowing and trampling, seed dispersal via long distance movements, and seed germination through trampling.

At the time of European settlement, bison were the largest herbivore on the Great Plains and the gray wolf was the largest carnivore. Lewis and Clark reported on the great herds of bison and their “shepherds” the wolves. Wolf densities may have been higher on the Great Plains than anywhere else on earth (Licht 1997*b*). Predator-prey studies and theory strongly suggest that wolf predation of bison almost certainly took a disproportionate number of less fit, young, and old animals. Therefore wolves affected bison genetics, demographics, and perhaps, other bison functions. Conversely, bison were the primary food for Great Plains’ wolves and are the primary reason for the incredible density of wolves that likely occurred in the region at the time of European settlement.

The records of early explorers support the hypothesis that coyotes were uncommon in the Northern Great Plains prior to extirpation of wolves. Under the protective umbrella of the large wolves, and in the absence of the mid-size coyote, small carnivores such as the black-footed ferret, swift fox, and ground-nesting ferruginous hawk prospered. They prospered in part because wolves, even at the high densities that occurred in the historic Great Plains, were less dense than modern coyote populations so they less frequently came across ferrets, swift fox, and ground-nesting ferruginous hawks. Furthermore, wolves probably had little interest in these species for food, nor were they well adapted to

catching them. In the case of the swift fox, the size disparity between wolves and the small fox is so great that there was probably little inter-specific competition. However, with the extirpation of the wolf from the Great Plains the coyote flourished as the top predator. In contrast to the wolf, the coyote is a severe mortality factor on ferrets, ground-nesting ferruginous hawks, and the swift fox. In the latter case much of the mortality appears to be due to inter-specific competition between the swift fox and the slightly larger coyote.

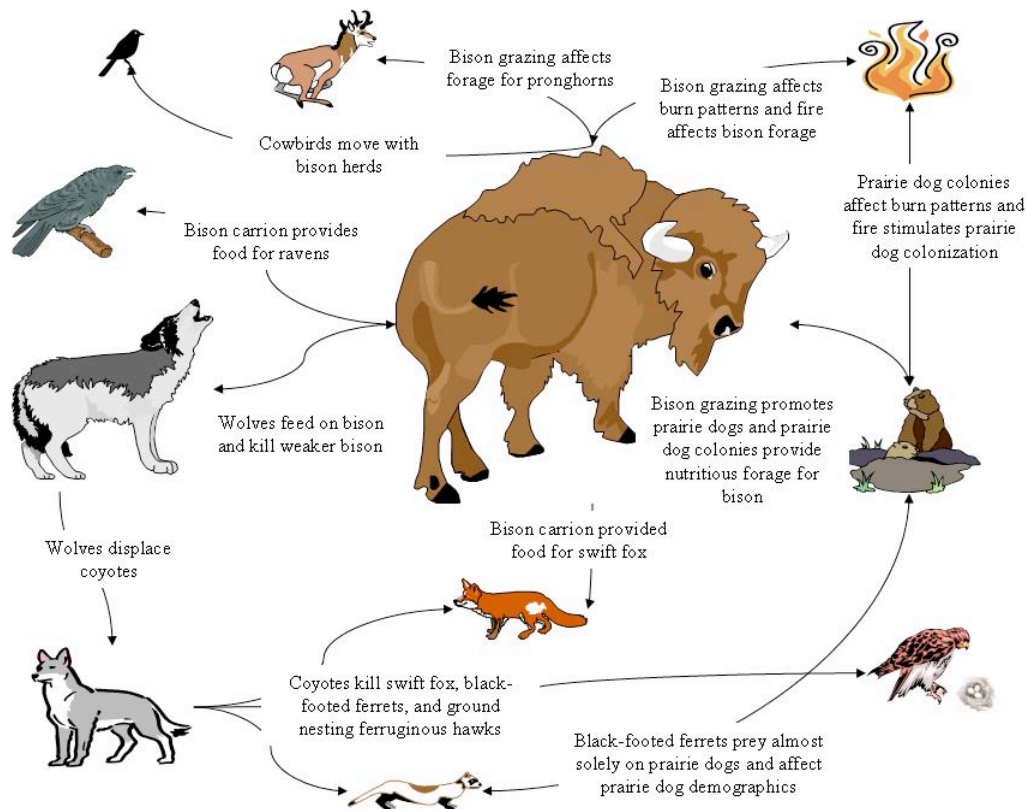


Figure B-30. Interactions of bison and other wildlife in the Northern Great Plains.

The incredible biomass of bison on the Great Plains, and the high densities of wolves, resulted in enormous amounts of carrion and nutrient cycling. In contrast, under current ranching operations, and even in National Park units and other protected areas, carrion is a missing resource and process in the Great Plains. The NPS units with bison all live-ship surplus animals to areas outside the park. Throughout the entire Great Plains the cycling of nutrients and minerals through bison has essentially stopped. This may affect soil quality and hence, have ripple effects up through trophic levels. The loss of carrion can also have a more direct effect. Ravens were historically the common corvid on the Great Plains and likely had a complex and dependent relationship with wolves and bison. It is

probably not coincidental that when wolves and bison were extirpated the raven also disappeared, although there was no deliberate effort to eradicate the species from the region. Similarly, the swift fox is a scavenger that likely benefited from bison carrion. This is probably especially true in the Northern Great Plains where other forage for the fox was rare or absent during severe winters with extended snow cover. It has been suggested that the loss of carrion may explain the disappearance of swift fox from the Northern Great Plains whereas they persisted in the Southern Great Plains.

Cowbirds also have a close historical relationship with bison. Cowbirds would accompany the vast herds of bison across the region, often perched on the backs of bison. As the bison moved, they flushed insects that are prey for cowbirds. The bison would also flush ground-nesting songbirds. The cowbirds would then parasitize the nest by leaving an egg, before continuing with the herds. It was a very efficient evolutionary strategy in the dynamic and mostly treeless Great Plains. The replacement of nomadic bison by sedentary cattle, and the increase in other food sources (e.g., small grains) and vertical structure (e.g., trees), has created ideal conditions for cowbirds to the detriment of many grassland passerines.

Another species that may be viewed as a keystone species, and has a very close mutualistic relationship with bison, is the black-tailed prairie dog. Heavy grazing by bison creates the short floral structure that is ideal for prairie dog colonization. Conversely, the burrowing, nutrient cycling, feeding, and other activities of prairie dogs create improved forage for bison, both in terms of nutritive value and plant phenology. Prairie dog colonies also positively affect many other species such as the black-footed ferret, swift fox, and ferruginous hawk by providing increased shelter, forage, and visibility.

Bison grazing, along with other grazing by other species, directly affects fire patterns. Fire has a complex and profound effect on grassland flora and fauna that extends well beyond the ability of any single conceptual model to fully capture. Fire effects are more fully described in some of the other models.

Conceptual Models for NGPN Cave Resources

In developing monitoring priorities at Jewel Cave and Wind Cave, we have attempted to summarize the cave resources at each park while considering the potential threats to these resources. At the same time, we have been diligent in teasing out those cave attributes that could be assessed for the purpose of monitoring cave ecosystem health over time. It is our hope that by monitoring cave water and meteorology, we will be able to capture any changes in cave status and elucidate trends in the associated indicators. The following narratives and tables shed light on the process and encapsulate our thoughts and findings.

Jewel Cave and Wind Cave Characteristics

Jewel Cave and Wind Cave are considered world class caves due to their unique features and background (Table B-2). Each park unit was established for the sake of preserving cave resources: Wind Cave was the first cave to be protected as a national park in 1903, and Jewel Cave was the first cave to be protected as a national monument in 1908. Both are considered to be some of the most complex network maze caves known to science (Palmer 2000). Jewel Cave is currently recognized as the world's second longest cave and Wind Cave is the fourth longest. Unlike many caves that were formed by surface waters running down through fractured limestone, these two caves were formed 40-50 million years ago by underground aquifers pushing up from below. Hence, the cave passages were created beneath the water table as the rock was dissolved. In addition to being some of the oldest caves identified, each cave is well known for the extensive deposits of secondary minerals (speleothems) that have formed in the caves since their origin: Jewel Cave passages are lined with calcite crystals (i.e., dogtooth spar), and Wind Cave has vast areas of raised and intersecting calcite veins (i.e., boxwork), giving the appearance of letter boxes or a honeycomb. In each case, these deposits are considered to be non-renewable resources given the environmental conditions and geological time required to form the minerals. Wind Cave is also the only federally owned cave where the Madison aquifer (the water table) can be directly accessed and hand-sampled in a four-state area. The Madison aquifer underlies North Dakota, South Dakota, Wyoming, and Montana, and covers nearly 11,000 km², and it is an important source of water for human use throughout the region (Carter et al. 2002). Given the suite of characteristics that these two caves possess, it was important to identify the primary stressors on these resources and look for attributes that could act as indicators of the health of the cave ecosystems.

Table B-2. Characteristics of Jewel Cave and Wind Cave.

Cave feature	Jewel Cave	Wind Cave
Anglo discovery	1900	1881
Federal designation	1908; 1 st cave in the U.S. to become a national monument	1903; 1 st cave in the U.S. to become a national park
Location	Black Hills of western South Dakota; 21 km (13 mi) west of Custer	Black Hills of western South Dakota; 13 km (8 mi) north of Hot Springs
Size of park unit	515 ha (1273 ac, or ~ 2 mi ²)	11,451 ha (28,295 ac, ~ 44 mi ²)
Cave footprint	~ 777 ha (~ 3 mi ²), and <i>ca.</i> 50 % occurs outside the park boundaries	~ 243 ha (~1 mi ²), 100 % occurs within the park boundaries
Substrate	Madison (Pahasapa) Limestone; ~ 137 m (450 ft) thick; cave occurs in the upper 250'	Madison (Pahasapa) Limestone; ~ 107 m (350 ft) thick; cave occurs in upper half
Origin	~ 40-50 million years before present	~ 40-50 million years before present
Formation	phreatic zone dissolution	phreatic zone dissolution
Depth	~ 186 m (610.0 ft)	~ 197 m (645.1 ft)
Length	~ 233 km (145 mi); 2 nd longest in the world	~ 209 km (130 mi), 4 th longest in the world
Geometry	Complex, three-dimensional rectilinear maze cave	Complex, three-dimensional rectilinear maze cave
Entrances		
•Natural		1
•Man-made	2	2
Blowholes		
•Natural		7
○ Enlarged	1 (i.e., the “historic entrance”)	1
Internal temperature	9.4°C (49°F)	12.2°C (54°F)
Outflow temperature	Yearly mean is 6.6°C (~ 44°F) (Pflitsch 2006)	Yearly mean is 10.8°C (~ 51°F) (Pflitsch 2006)
Airflow pattern	Barometric ($P_{atm} \uparrow$, airflow in; $P_{atm} \downarrow$, airflow out), and without seasonal variability (Pflitsch 2006).	Barometric, and variable by seasons: winter, airflow mostly in; summer, airflow mostly out (Pflitsch 2006).
Biota	The largest known hibernaculum for Townsend’s big-eared bats, which are not historic residents.	No cave-adapted life forms are known to occur in the cave.
Speleothems	Best known for the calcite crystals (dogtooth spar) that line the cave passages. Other deposits include hydromagnesite balloons, helictites, anthodites (frostwork), and gypsum hairs and flowers.	Best known for the extensive deposits of calcite boxwork in the cave. Other deposits include helictite bushes, anthodites (frostwork), and gypsum hairs and ropes.
Groundwater		
•Drip sites	50+	~ 1460
•Perched pools	Yes, a few	~ 200
•Streamlets	None	3 perennial
•Lakes	None: The cave is not known to intersect the Madison aquifer	8 named, and many unnamed lakes occur where the cave intersects the Madison aquifer; the total number fluctuates with the water table

Jewel Cave and Wind Cave Stressors

Generally speaking, a cave is a relatively stable environment by nature, but one that is normally devoid of long-term human presence and continual use. Hence, cave managers are always concerned about impacts on cave resources from visitors, staff, and cave explorers as they tour, work, or travel in the cave. These impacts can include the input of foreign material, disturbance or damage to cave surfaces and speleothems, modification of the cave atmosphere by the addition of carbon dioxide, moisture, and heat from human presence, or artificial lighting, or changes in cave temperatures and airflow by modifications to natural entrances, or the construction of man-made entrances. Human activity on the surface can also affect cave resources through infiltrating pollutants from roads, parking lots, and faulty sewer systems, or herbicides from exotic plant treatments. Prescribed fire and mechanical thinning can change tree density and cover and affect surface hydrology, while ash from forest fires can contribute to heavy metal concentrations in runoff (Kelley et al. 2006). At a larger scale, landscape and land-use changes, in the form of residential developments in associated watersheds or water withdrawal from underlying aquifers, can potentially impact the cave environment. Global climate change is also looming on the horizon with potential changes in ambient temperature or precipitation patterns, and air pollution from regional energy development is also a concern. These were some of the issues addressed by the NGPN staff and cave personnel when examining what might influence or disturb the cave systems at Jewel Cave National Monument and Wind Cave National Park.

Tables B-3 through B-6 are the result of a brainstorming effort in which we have thought widely about potential stressors and attributes for monitoring, including secondary variables that could be considered along with primary candidate indicators. In this case, Table B-3 purposely list things that have been ruled out as high priorities (e.g., variables related to bats). “Stressor categories” in column 1 match what we used in Chapter 2 for presenting similar tables about general NGPN stressors. Table B-4 is a supplementary table that specifically addresses cave air flow and microclimate, and associated indicators, given potential impacts on these variables; and, likewise, Table B-5 is a supplementary table that specifically addresses cave water input, and associated indicators. Lastly, Table B-6 (see the *Jewel Cave and Wind Cave Potential Monitoring Attributes* section below) focuses on attributes in an effort to identify a valuable subset that could act as indicators of cave condition over time.

Jewel Cave and Wind Cave Potential Monitoring Attributes

For several months NGPN staff and park staff conducted an ongoing discussion regarding the pros and cons of various cave attributes that might act as appropriate indicators of cave condition and integrity (Table B-6). Many of these items were determined to be less than ideal for long-term monitoring because they were weak indicators of cave ecosystem health (e.g., ozone, SO_{2g} and CO_{2g}), were being addressed via other practices at the park (e.g., radon, foreign material input, and algal growth), or were deemed to be too vague, given our current knowledge, to be used as an indicator (e.g., speleothem formation/degradation and microbial community composition and trophic structure).

Table B-3. Potential stressors on cave resources at Jewel Cave and Wind Cave.

Stressor Category	Specific Stressor	Impacts	Indicators
Global atmospheric changes	Surface air quality: Increased surface atmospheric concentration or changes in deposition of CO ₂ , N, SO ₂ , or ozone	Any potential effects are speculative and probably very unlikely. Likelihood of any significant impacts is unknown, and this is a low concern to JECA and WICA cave experts. Perhaps could lead to changes in cave air or water composition and solution chemistry*. (E.g., increased acidity of water could result in dissolution effects on cave formations.) However, cave is buffered by limestone strata, making infiltration of more acidic water unlikely.	Deposition at surface stations; chemical properties of cave water; air composition in cave; rate of formation/degradation of sensitive geological features.
	Warmer winter and/or summer temperatures and altered precipitation amount and patterns; changes in average surface wind conditions	Surface climate changes lead to changes in cave temperature, relative humidity, airflow characteristics (volume, speed, and direction of flow), drip inflow amount, number of drip sites, and aquifer recharge rate. Surface water flow and net evapotranspiration could increase or decrease, leading to drier or moister conditions in cave*. Higher winter temperatures could cause higher metabolism of hibernating bats, leading to winter mortality or stressed body conditions at emergence.	Weather/climate data from surface station in park and regionally; microclimate changes in cave*; changes in cave hydrology**; changes in bat community (number, roost selection, within-winter activity, mortality, pregnancy success, body mass at emergence).
Altered disturbance regime	External fire suppression, increased high-intensity fires, altered grazing/browsing, increased incidence and spatial extent of mountain pine beetle infestations, and other disturbances (e.g., diseases) affecting tree density and understory cover	May affect net infiltration of water into soil by altering run-off and evapotranspiration (see “Altered hydrology”). Changes in soil chemistry due to Jasper Fire or future large-scale fires <u>may</u> lead to changes in concentrations of nitrate, phosphate, sulfate, basic cations, and heavy metals (e.g., mercury, cadmium, and arsenic) in water (Debano et al. 1998; Kelly et al. 2006; Woodruff et al. 2002) entering cave.	Composition and distribution of plant community types; woody species composition and diameter/density distributions. Changes in cave hydrology**.
Altered hydrology and geomorphology	Groundwater withdrawal	May alter aquifer levels in Wind Cave, and would indicate potential threats to springs and streams in the park and region. Within the cave, reduced cave-lake levels could affect localized microbial communities.	Cave-lake levels and areal extent; groundwater withdrawal rates in the region; water level in park wells and other wells in the region; spring discharge.

Table B-3. Potential stressors on cave resources at Jewel Cave and Wind Cave (continued).

Stressor Category	Specific Stressor	Impacts	Indicators
Altered hydrology and geomorphology	Secondary hydrologic effects of other park-surface stressors and landscape changes	Surface changes in run-off, evapotranspiration, and creek flow may lead to changes in cave water level, water drip inflow rates, number of drip sites, water availability near drip sites, recharge rate of aquifer, and cave lake water levels**.	Cave hydrology**. Surface spring occurrence and discharge; flow patterns in surface streams of park and surrounding region.
Chemical inputs and pollution	Metals, pesticides, antifreezes, other hydrocarbons and arsenic originating on surface in or near park	Contaminated ground water. Biggest concern is the degradation of water quality for its own sake; effects on cave biota and other resources could occur. Associated surface-water contamination could threaten amphibians, invertebrates, and other wildlife using water bodies. Ultimately, aquifers might be compromised and local citizens put at risk.	Amount and location of herbicides sprayed in park and surrounding areas; occurrence of spill events; presence of contaminants in springs, drip sites, streamlets, and aquifer; changes in cave microbial communities near water sources; vehicle traffic on local highways.
	Human waste is a concern at both parks from leaking sewer pipes, possible sewage dumping (JECA), and upstream pollution from septic fields (e.g., Beaver Creek drainage at WICA)	Degrades cave water quality, surface water sources, and aquifer. Associated surface-water contamination could threaten some wildlife species. Localized effects on microbe community near cave lakes are uncertain but could occur.	Presence of fecal pollutants in springs, streams, and cave water sources; presence and characteristics of sewage spill events and treatment areas; changes in cave microbial communities if any depend on pristine water.
Landscape changes	Development adjacent to park; changes in adjacent grazing, timber harvest, mining, etc.	Changes in water withdrawals and surface hydrology (e.g., run-off, evapotranspiration) alter aquifer level and direct drip inputs (see "Altered hydrology"). Pollutants from roads, parking lots, septic systems, pesticide application, etc., may enter cave via aquifer or direct water inputs, potentially with localized effects on cave biota (see "Chemical inputs").	Changes in land cover and general land uses around park; see previous entries for associated indicators relating to hydrology and pollutants.

Table B-3. Potential stressors on cave resources at Jewel Cave and Wind Cave (continued).

Stressor Category	Specific Stressor	Impacts	Indicators
Human use of parks and management	Direct material inputs and disturbance in the cave by park staff and visitors	Human use leads to inputs of skin cells, fibers, larger debris, and microscopic life (dust mites, algal spores), increasing net energy availability and introducing springtails, algae, cyanobacteria, and other biota, thereby altering native biota and increasing trophic complexity and energy-flow dynamics. Human presence leads to direct disturbance (accidental, theft, vandalism) of secondary mineral deposits such as speleothems and corrosion residues. Cave exploration may enlarge small passages, further changing microclimate.	Dust and biotic deposition rates; trophic structure; presence of algae and non-native taxa; rates of loss or degradation of sensitive or high-interest cave features along visitor routes and high-impact portions of survey routes; changes in airflow patterns in cave interior.
	Effects of human entrance on cave atmosphere	Human entrance leads to altered patterns of air flow (e.g., increased inflow of surface air), increased temperature, local or cave-wide changes in relative humidity*, and atmospheric composition; the last impact is very unlikely as human CO ₂ input rates appear to have no effect on air composition near survey routes.	Microclimate characteristics* along tour routes vs. undisturbed areas; number of visitors; changes in entrance airflow patterns.
	Cave-tour infrastructure	Lights increase temperature and provide artificial light along tour routes, allowing algae to develop.	Microclimate characteristics* along tour routes vs. undisturbed areas; algae presence near lights; number/type of lights and heat output.
	Mechanical thinning or prescribed fire	Changes in tree density may alter surface hydrology, with resulting effects on cave hydrology (see "Altered hydrology").	See "Altered disturbance regimes." Mapping and documentation of disturbance characteristics.

Table B-3. Potential stressors on cave resources at Jewel Cave and Wind Cave (continued).

Stressor Category	Specific Stressor	Impacts	Indicators
	Exotic plant treatments	Herbicides may enter cave through aquifer or drip input. See "Chemical inputs."	See "Chemical inputs." Area of exotic treatments; amount and type of herbicides used.
	Surface infrastructure	Pollutants from roads, parking lots, and sewer systems may enter cave directly from surfaces at JECA or WICA or via secondary input through aquifer (see "Chemical inputs"). Roads and parking lots may alter surface run-off, affecting cave hydrology (see "Altered hydrology").	See "Altered hydrology" and "Chemical inputs." Extent of surface infrastructure; hydrological patterns of parking lots or other impermeable areas.
Altered abundance of biota	Introduced species	Humans act as vectors for springtails, algae, cyanobacteria, and other biota to colonize the cave; other changes to the cave environment may allow these biota to persist and increase. As a result, community composition is altered, and trophic structure made more complex.	Trophic structure; occurrence of native microbes; occurrence of introduced taxa.
	Decreased occurrence or local extinction of native microbes	Loss of native biodiversity; conceivably some taxa could be globally unique. Formation of corrosion residues, which are produced by and encrust native cave microbes (Barns et al. 2003) would be diminished.	See "Introduced species." Loss or degradation of corrosion residues.

*See Table B-4 for general potential impacts of altered cave air flow and microclimate, and associated indicators.

**See Table B-5 for general potential impacts of altered water inputs, and associated indicators.

Table B-4. Potential effects and indicators of changes in cave airflow.

Impacts	Indicators
<p>May alter the mean, variability, and rate of change in cave temperature and relative humidity, as well as cave heat transfer and moisture exchange with the atmosphere. Increased temperature could lead to drier conditions. These changes alter the fundamental stability of the caves that the parks are striving to maintain. Changes in temperature and relative humidity may affect chemical reactions building or maintaining speleothems, and alter suitability for native and exotic biota. Also, airflow (i.e., air exchange with the surface) may influence the concentration of trace gasses, such as radon and carbon dioxide, in the cave. Higher concentrations of carbon dioxide gas in the cave atmosphere, due to diminished airflow, may inhibit speleothem formation by altering the equilibrium dynamics of calcium carbonate precipitation (i.e., as water saturated with calcium bicarbonate evaporates, carbon dioxide is given off—so high concentrations of this gas in the cave atmosphere could slow the precipitation process), and high concentrations of radon could be hazardous to employee and visitor health.</p>	<p>Microclimate indicators include patterns of airflow volume, direction, temperature, and moisture content at cave entrances and elsewhere in cave; temperature/relative humidity gradient from entrance into cave; temperature near hibernating bats and deeper in cave.</p>

Table B-5. Potential effects and indicators of changes in cave water inputs.

Impacts	Indicators
<p>Changes in water inputs (cave lake water level, number of drip sites, net drip input and water availability), water chemistry, relative humidity, and temperature may increase rate of precipitation or dissolution of specific speleothems, particularly sensitive features. Changes in water availability, relative humidity, light, and temperature may alter native microbial abundance / community composition, or lead to increased occurrence of springtails, algae, cyanobacteria, and other biota that colonized the cave due to human presence. The simple cave trophic structure / energy flow may be altered, particularly by becoming more complex through the addition of trophic levels.</p>	<p>Hydrologic indicators include aquifer water levels; levels measured in park and outside-park wells; withdrawal rates; occurrence and volume input of drip sites; occurrence and flow of streamlets; occurrence and flow of external springs; rate of external stream flows.</p>

Table B-6. Cave attributes considered for potential monitoring in Jewel and Wind Caves.

Attribute (park relevance)	Rationale for monitoring	Rationale for not monitoring
<i>Cave Air Composition and Climate</i>		
Radon (JECA, WICA)	High radon levels can be human health issue for visitors and park staff.	While radon is a naturally occurring human health threat, it is not an ecosystem stressor. Both parks have assessed radon levels in the past and found them to be stable and moderate, but each will continue to sample periodically as recommended by the National Caves Association guidelines.
Composition of CO ₂ , SO ₂ , ozone, and other gasses within various zones of the cave (JECA, WICA)	Surface atmospheric changes could lead to increases in CO ₂ and SO ₂ within the cave and potentially affect carbonic or sulfuric acid concentrations, or otherwise slow the growth of speleothems by altering the chemical equilibrium associated with calcium carbonate deposition. Ozone is a phytotoxic air pollutant that can be dispersed over long distances, and is of concern to many parks.	Atmospheric concentrations of CO ₂ and SO ₂ are not expected to increase enough to significantly impact cave biota or features, and ozone is primarily a threat to terrestrial plants, which do not exist inside the cave.
Temperature, relative humidity: average and variability, within various zones of the cave (JECA, WICA)	These parameters affect rate of change of sensitive cave speleothems, suitability for native microbial life, rate of increase of introduced algae/microbes, and (at hibernacula) over-winter success of bats. Along with water, they are the fundamental influences on the internal cave and likely indicator of cave ecological health (Toomey 2006). Changes within the cave may be good indicator of global climate change effects on the cave. Affected, at least locally, by amount of human use of the cave. Solid baseline data for long-term monitoring. In conjunction with volumetric airflow rate, these measures can be used to determine the net exchange of cave moisture and cave heat with the atmosphere.	Instead of monitoring temperature and RH, we could directly monitor cave elements that would be stressed by changes in these parameters. Although microclimatic changes in the cave would be another interesting/worrisome effect of global climate change, the value of cave climate as a sensitive indicator of global change is questionable, and we already have long-term high quality stations that are capturing trends on the surface despite extremely high temporal variability.
Airflow: Distribution of speeds and direction (e.g., % inflow vs. outflow), within various zones of the cave (JECA, WICA)	Airflow is of high interest for how the cave functions. It influences temperature and RH, especially near the entrances, and is a determinant of how much heat and moisture are exchanged with the external environment. There is solid baseline data for long-term monitoring. Entrance and visitor management may affect airflow.	There is not a clear link between changes in air flow and changes in RH and temperature deep in the cave.

Table B-6. Cave attributes considered for potential monitoring in Jewel and Wind Caves (continued).

Attribute (park relevance)	Rationale for monitoring	Rationale for not monitoring
<i>Cave Geological Features</i>		
Total passage length; physical mapping (JECA, WICA)	These define the cave system.	Ongoing cave inventories and surveys already track these attributes adequately.
Occurrence and rate of formation/degradation of specific speleothems (JECA, WICA)	Unique, world-class features are present. These may be affected by changes in microclimate, air flow, water chemistry, and visitor use. If the rationale for tracking microclimate is partially due to the effects it may have on specific components, these features should also be monitored.	Formation and degradation are natural processes that are not formulaic, and the rate of change is very slow for most features (although some could be photographed every decade or so). It is difficult to choose what to measure.
<i>Cave Aquatic Systems</i>		
Aquifer level and spatial extent (WICA)	WICA cave lakes are the only places where the Madison aquifer is directly accessible on federal lands. The aquifer is of high importance for regional water flows and for human use, and may be affected by changes in water use from throughout the region, as well as surface changes in climate, land use, and hydrology.	Some monitoring already occurs via the park drinking-water well that taps into the Madison aquifer, but water level changes in the park well often do not match changes measured in the cave lakes (Ohms 2004).
Aquifer physical and chemical characteristics (WICA)	The aquifer is an important source of drinking water throughout the region, and may be affected by pollutants. These attributes would be indicators of the overall health of the aquifer and can alert managers in the region to ongoing contamination and other changes.	Some monitoring already occurs via a park well that penetrates the Madison aquifer. No cave organisms are known to be dependent upon the lake system; however, some microbes may exist there.
Water drip inputs: number of drips, total input, chemical composition, potentially in different zones of cave (JECA, WICA)	Potential source of pollutants affecting cave ecosystem; can provide early warning of pollutants (e.g., antifreeze, <i>E. coli</i> , nitrates, hydrocarbons) entering groundwater from surface, and indicate changes in surface land management. Changes in water input and water chemistry may affect features via the processes of dissolution and precipitation. Cave microbes would also be affected, as most are probably limited to areas with water. Water drip inputs may influence cave RH.	Total input and effects on RH and cave formations are minimal and localized.

Table B-6. Cave attributes considered for potential monitoring in Jewel and Wind Caves (continued).

Attribute (park relevance)	Rationale for monitoring	Rationale for not monitoring
<i>Biota</i>		
Native microbes and trophic structure, potentially in different zones of cave (JECA, WICA)	Fundamental component: simple trophic structure characterizes the cave interior ecosystem. Potentially unique organisms.	Not well understood; microbial species and communities are poorly defined, and no cave-specific microbes have ever been found in the caves. Lab culture or isolation techniques limited. This would really be an investigative inventory at this stage; one that is better suited for research.
Hibernating bats (JECA)	Of high significance for regional bat conservation. Sensitive to disturbance and changes in microclimate.	Present due to human modifications of cave entrance; not a fundamental part of the “natural” (historical) cave ecosystem. Extensive habitat for bats occurs in surrounding caves and forest. Already indexed by annual JECA surveys.
Introduced algae, invertebrates, microbial life (JECA, WICA)	Non-native; produce changes in trophic structure or interactions by increasing trophic complexity; alter the environment (e.g., turn rocks green). Affected by visitor direct inputs and indirect effects (altered RH, light sources). Could continue to increase due to human use, changes in microclimate or energy availability.	The extent of algal growth is assessed during periodic treatments to remove the organisms from cave surfaces.
Mice, woodrats (JECA, WICA)	Deposit hantavirus around the cave entrance; bring in some material and nutrients to the near-entrance portions of the cave.	Not a fundamental part of the cave ecosystem away from the entrances; probably no effect on internal cave system. Species present are very common and widespread in western US.
<i>Other Human Effects</i>		
Damage or removal of speleothems (JECA, WICA)	Degrades unique geological resources.	This is a security issue already being addressed by the parks.
Introduction of debris and increased dust levels (JECA, WICA)	Human inputs (skin cells, hair, dust mites, algal spores) alter the basic trophic structure of the cave ecosystem. Water condensing on settled dust can increase dissolution of formations. Lint, trash, gum, etc. degrade the cave visually. Reducing inputs is a management priority, and continual use of caves will require continual mitigation.	Cave cleanup programs in place, and the caves periodically conduct specialized monitoring for lint and dust along travel routes.
Cave lights (JECA, WICA)	Create local hotter and drier spots; heat and light encourages growth of algae not native to cave.	Already addressed through park studies; effects on cave are localized.

NGPN Aquatic Systems

General Model of NGPN Aquatic Drivers and Stressors

The Aquatic Resources General Conceptual Model for the Northern Great Plains Network parks was developed by Joyce Williamson and Barbara Rowe, USGS South Dakota Water Science Center (Figure B-31). An important goal of this conceptual model was to depict how the large scale, external drivers (major forces of change) such as climate, landform, time, upland watershed characteristics, and human sociology affect the ecosystem structure and function. In addition, the model summarizes the major categories of stressors affecting Network aquatic systems and the general attributes of these systems that respond to drivers and stressors. These attributes are discussed further in the context of potential monitoring measures for NGPN aquatic systems (Table B-7). Below, we briefly discuss major drivers and stressors affecting NGPN aquatic resources.

Climate: The Northern Great Plains is characterized by extremes in climate with hot, dry summers and cold, snowy winters. In addition, climate in this region experiences a great deal of annual variation with drought cycles occurring approximately every 20 years (Hinckley 1995). Furthermore, climate change could have dramatic impacts on the aquatic ecosystems of the Northern Great Plains, potentially causing early snowmelt runoff, reduced stream flows, warmer water temperatures, and decreased water quality (Poff et al. 2002).

Landform, time, and upland watershed characteristics: Much of the Northern Great Plains is relatively flat. The Rocky Mountains to the west are the primary reason for the arid to semi-arid conditions on the plains. Because of regional landform, soils, and climatic patterns, rivers of the Great Plains generally flow west to east and have high turbidity and evaporation rates, moderate flow velocity and dynamic channels (NSP 2005b). Likewise, the prairie streams are characterized by variable flow regimes. Furthermore, many first- and second-order streams in prairies occur in areas devoid of trees. The lack of vegetative inputs (i.e., leaves and woody debris), combined with frequent and prolonged dry periods and periodic scouring floods, allow for little in-stream decomposition (Matthews 1988).

Human sociology: Given the scarcity of water resources in the plains, many of the Native American and early Euro-Americans settled near flowing rivers. After the turn of the century, the Euro-American settlers in the Great Plains developed a strong, agrarian culture, despite the fact that much of the area is poorly suited to cultivation. These changes as well as the ever changing economy and society of the U. S. over the last few centuries have dramatically influenced water resources in the Northern Great Plains, as discussed below.

Stressors: These external, primarily abiotic, forces influence the regional external and within park stressors (human-caused perturbations or natural events that are applied at excessive or deficient levels [Barrett et al. 1976:192]) which in turn impact the aquatic resources. Many of the

stressors for the Network aquatic resources occur outside the park boundaries. For example, most of the rivers within the network have altered flows due to dams constructed up river. Dams are a major stressor of natural resources at seven of 13 parks within the NGPN (Fort Union Trading Post NHS, Knife River Indian Villages NHS, Devils Tower NM, Fort Laramie NHS, Scotts Bluff NM, Niobrara National Scenic River, and Missouri National Recreational River). In addition, another critical stressor, water diversions for irrigation and groundwater withdrawals, are impacting the Niobrara River parks (AGFO, Niobrara National Scenic River, and Niobrara River part of MNRR) and potentially the Little Missouri River at Theodore Roosevelt NP and the cave lakes at Wind Cave NP. Additional regional stressors that park managers have little influence over include pollution from surrounding agriculture in the form of pesticides and herbicides as well as pollution from the increasing number of coal-fired power plants (currently 30 are operational and 23 new plant are proposed for the Dakotas, Nebraska, Montana, and Wyoming [NETL 2007a, b]) being constructed upwind of most Network parks. Recent research conducted by USGS scientists has identified atmospheric deposition as the prominent mercury input for stream systems (Marvin-DiPasquale et al. 2009). Finally, many parks are concerned with adjacent residential and hobby-farm development, especially Scotts Bluff NM.

Potential effects can also occur as a result of within-park stressors and management. The larger parks within the Network such as Theodore Roosevelt NP and Badlands NP have large herds of ungulates, both native (bison) and non-native (feral horses). Currently these parks are often restrained from reducing their herd size due to threat of Chronic Wasting Disease. Concentration of large herds confined to the boundaries of the parks can potentially increase erosion and decrease water quality especially levels of fecal coliform. Throughout the Network exotic plant species such as saltcedar (*Tamarix* spp.) also act as stressors to the system. For example, saltcedar excretes salts that are deposited on the soil surface under the plant inhibiting germination and growth of competing species and for its very great consumption of water, as much as 760 L of water a day (Di Tomaso 1998). As a result, saltcedar infestations significantly alter the hydrology of an area (Di Tomaso 1998).

Figure B-31. Drivers and major stressors of NGPN aquatic systems.
Source: U.S. Geological Survey South Dakota Water Science Center.

Ecosystem Process Model for NGPN Streams and River

As a framework for understanding and discussing major components and processes of NGPN stream and river ecosystems, the NGPN adopted and modified the stream ecosystem function model developed by Scott et al. (2005). This model (Figure B-32) shows the key drivers, processes, and relationships in stream and river systems.

Streamflow regime, stream geomorphology, and water quality are major factors influencing stream ecosystem function. Stream flow originates from rainfall within a watershed (M. Bynum, NGPN, pers. comm.). This rainfall reaches a stream or river via direct precipitation, overland flow, and groundwater flow. During a rainfall event, peaks in storm flow can occur on top of the stream's normal flow. This streamflow regime determines the physical forces available in a drainage to erode, transport and deposit sediment and maintain/modify the stream/river channel. Stream flow and sediment inputs are affected by upland and riparian watershed characteristics. Changes in vegetation cover due to natural disturbances (fire) or human use (development) may increase the magnitude of peak flows and erosion inputs. Both the variations in stream flow and the size and amount of sediment supplied to the stream from the watershed can modify the stream/river channels. These factors are determinants of the stream width, depth, and the formation pools, riffles, meander loops, and sand bars which are important habitat for aquatic biota (Gordon et al. 1992).

Indeed, prior to dam construction and channelization of the Missouri River, high, fast seasonal pulses of water scoured sandbars and shorelines clean. Construction of dams along the river has limited these pulses so that the originally wide river channels with scattered, sparsely vegetated sandbars have turned into narrower, more forested corridors. The endangered least tern (*Charadrius melodus*) and piping plover (*Sterna antillarum*) favor these sandbars free of vegetation so they can see approaching mammalian predators. In addition, water levels behind dams on the Missouri River generally are kept high, flooding nesting areas. Another critically endangered species in the Missouri River system is the pallid sturgeon (*Scaphirhynchus albus*). This sturgeon evolved with the diverse Missouri River system when flood plains, backwaters, sandbars, and braided main channel waters formed this large-river system. Pallid sturgeon habitat has been modified through river channelization, construction of dams, and related changes in water flow. This highly altered hydrograph prevents pallid sturgeon migration movements and has destroyed or altered its spawning grounds. The Missouri River water has less turbidity now than under natural conditions. Pallid sturgeon require turbid waters where predators are less likely to find it (see Hesse and Sheets 1993).

Besides the streamflow regime and the stream geomorphology, water quality also plays an important role in stream function. Water temperature affects the growth and respiration of organisms and the productivity of ecosystems. Temperature can influence organisms directly or indirectly due to changes in oxygen saturation levels (Thorp and Covich 2001). Increase in salinity and alkalinity and decreases in dissolved oxygen were found to be correlated with decreases in macroinvertebrate density and diversity (Earl and Blinn 2003). In addition,

anthropogenic pollution has an impact on the integrity of aquatic resources by altering the chemical parameters (Thorpe and Covich 2001).

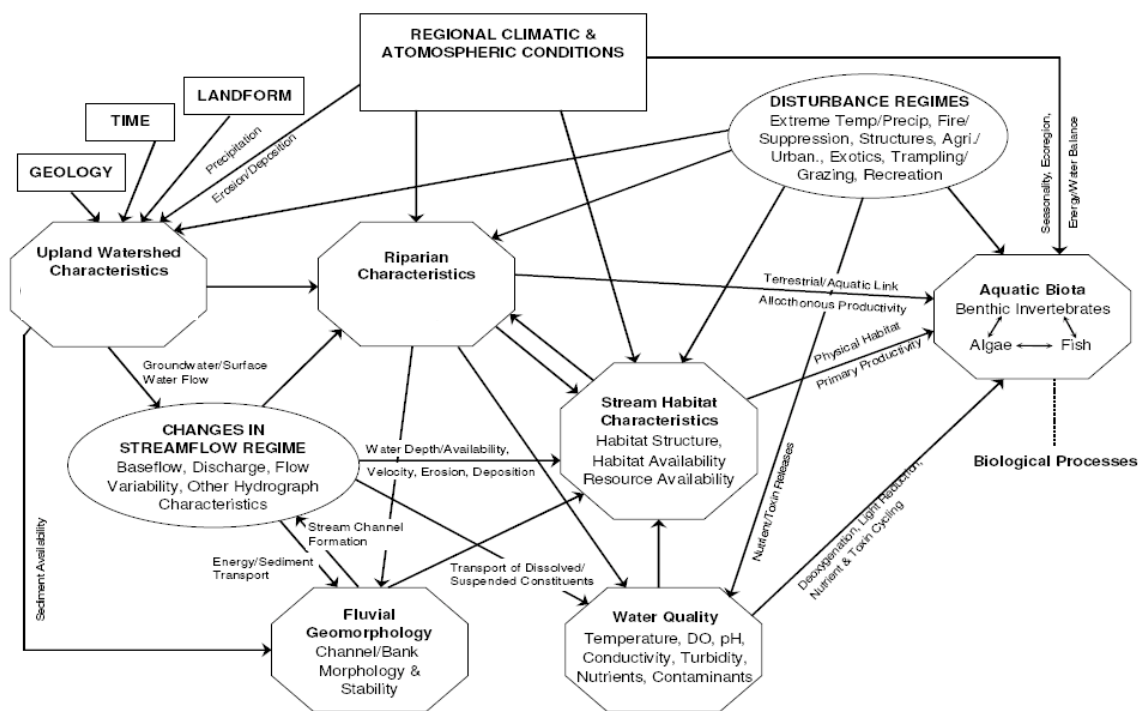


Figure B-32. Ecosystem model for river/stream systems.

Rectangles indicate major drivers of ecosystem change and variability. Hexagons indicate major ecosystem components and processes (attributes). Arrows indicate ecosystem stresses and responses (functional relationships). The model is constrained by global climatic and atmospheric conditions, topography, parent (geologic) material and potential biota. Source: NPS (2008); modified from Scott et al. (2005).

Summary of Potential Monitoring Measures for NGPN River/Stream Systems

Indicators are a set of monitoring attributes that are particularly information-rich in the sense that their values are somehow indicative of the quality, health, or integrity of the larger ecological system to which they belong (Noon 2003). A set of potential monitoring indicators for the river/stream systems includes water quality (physical properties, water chemistry, and aquatic macroinvertebrates) water supply, and stream sediment and geomorphology (Table B-7). Each indicator has numerous specific measures that can be taken, which provide specific information about the health of NGPN aquatic systems.

Water quality:

- The physical properties are the core water quality parameters. Ongoing monitoring of these constituents measure water body response to the environment and may qualify and quantify changes. Dissolved oxygen, pH, specific conductance, and water temperature are required sampling core water quality parameters. Aquatic organisms are dependent on specific ranges of these parameters for their optimum health and survival.
- Water chemistry focuses on the microorganisms, nutrients, pesticides, petroleum hydrocarbons, and trace metals that can potentially contaminate the systems. Monitoring of water chemistry provides concentrations of select constituents that may affect water quality, microorganisms, macroinvertebrates, plants, and fish. Although sometimes costly, water quality monitoring may define specific impacts to the system and can potentially document recovery of contaminated systems.
- Macroinvertebrates are abundant in most streams, reasonably easy to collect, and good indicators of localized aquatic conditions. Monitoring results can be used for assessing aquatic conditions at multiple reference sites within the same stream and for temporal variations. Because macroinvertebrates have limited migration patterns, they are well suited for assessing site-specific conditions. With complex life cycles of about 1 year, macroinvertebrates integrate the effects of the environmental variations and can respond quickly to stressors.

Water supply: Monitoring of water supply provides information regarding climatic cycles or long-term changes, as well as land- and water-use influences and management practices. Typical measures of water supply are flow/discharge of streams and levels of lakes for surface water, and static levels of wells for ground water.

Stream sediment and geomorphology: Monitoring of changes in the bed or the bank of a stream may be indicators of the stream response to changes from natural and anthropogenic influences and may influence the aquatic systems. Field measurements and aerial imagery can document changes in stream geomorphology. Finally, bank erosion as part of the river geomorphology poses a threat to the cultural elements at Fort Union Trading Post NHS and Knife River Indian Villages NHS.

Table B-7. Potential indicators and measures for NGPN aquatic resources.
Source: U.S. Geological Survey South Dakota Water Science Center.

Indicator / Measures	Description of information provided by measures
<i>Water Quality: Physical Properties</i>	
Dissolved oxygen	Dissolved oxygen concentration (DO) is a measure of the amount of oxygen in the water column. DO in rivers and streams typically declines as temperature increases and as flow decreases, and also responds to photosynthesis resulting in natural variation during the day and additional natural variation through the season. DO in water can vary over extended periods of time due to changes in the landscape or climate. DO levels are considered an important indicator of a water body's ability to support aquatic life.
pH	pH is a measure of the hydrogen ion concentration in a solution. pH values of less than 7 indicate that water is acidic, a pH value of 7 indicates that water is neutral, and pH values greater than 7 indicate that water is alkaline. Surface waters typically range from 6.5 to 8.5 and rainfall is more acidic (around 5). Changes in pH may provide indications of changes in the source water and within the watershed. The pH is also dependent on atmospheric deposition (acid rain) and the composition of the surrounding rock. Different organisms flourish within different ranges of pH.
Specific conductance	Specific conductance is a measure of the water's ability to conduct electricity. Concentrations of specific conductance typically are proportional to the dissolved major ions in the water such as calcium, magnesium, sodium, and sulfate. A change in specific conductance is an indication of a change in the concentrations of these various major ions. Small changes in specific conductance also are common through the day and through the seasons.
Temperature	Water temperature is affected by solar radiation, air temperature, rainfall, flow dynamics, physiography of the water body (i.e., depth), and the amount of development in the watershed. Water temperature monitoring indicates response to daily and annual climatic variations and may track short-term drought or long-term climate changes. Temperature can also be an indicator of changes in water use, source, and flow dynamics. Aquatic organisms are dependent on specific temperature ranges for their optimum health and survival.
Turbidity	Turbidity is a measure of the clarity of water. It can be used as a surrogate to estimate concentrations of suspended sediment and/or organic matter within a stream and has been used in some situations to estimate bacteria or nutrient concentrations. High concentrations of particulate matter can cause increased sedimentation in a stream and can also affect aquatic life.

Table B.7. Potential indicators and measures for NGPN aquatic resources (continued).

Indicator / Measures	Description of information provided by measures
<i>Water Quality: Water Chemistry</i>	
Bacteria/microorganisms	Various bacteria (e.g. fecal, and streptococci) may be indicators of impacts or influences associated with human or animal waste. Bacterial concentrations typically are greatest during storm events when soils near streams are flushed by higher water levels or heavy rainfall. High bacterial concentrations in groundwater could indicate contamination resulting from anthropogenic sources, such as septic systems.
Nutrients	Nutrient concentrations can provide indications of natural levels driven by hydrogeologic factors, and by anthropogenic activities such as fertilizers associated with agricultural land-use practices, landscaping activities, or effluent from septic systems. Examples of nutrients include nitrate, nitrite, and phosphorous.
Pesticides	Pesticides are indicators of anthropogenic activities. The use of herbicides for weed control in- and adjacent- to park land could impact the quality of water. Herbicides and insecticides are associated with a variety of agricultural and non-agricultural practices. Some pesticides have been associated with mutagenetic changes in aquatic organisms. Examples of pesticides include metachlor and atrazine.
Petroleum hydrocarbons	Petroleum hydrocarbons may be indicators of water contamination by fuel from motorized vehicles. Gasoline and diesel hydrocarbons are the main components of the fuel that is used in most motorized vehicles. Contaminant residue from fuel leaks and spills is trapped in the pore space of concrete and asphalt. Storm water can flush these contaminants from parking lots and highways to streams, caves, and aquifers. Examples of petroleum hydrocarbons include benzene and toluene.
Select trace metals	Metals are naturally occurring in the environment; however, changes in measured concentrations of metals in water may be an indicator of changes in land-use practices. For example, selenium is often linked to impacts from irrigation where above normal water on native soils can flush the selenium from soils and into streams. Trace metals of greatest concern are those that have impacts at high concentrations such as arsenic, mercury, and selenium.

Table B.7. Potential indicators and measures for NGPN aquatic resources (continued).

Indicator / Measures	Description of information provided by measures
<i>Water Quality: Aquatic macroinvertebrates</i>	
Counts	The total number of individuals, the number of taxa identified, and the number of individuals within each taxa can provide indication of the richness or diversity at a site. These counts typically decrease if the site is disturbed or impaired. Actual counts will vary with sampling methods so comparison from one year to another may not be valid if the sampling methods are not similar.
Dominant species	The species, particularly the dominant species, that are identified at a site are indicators of stream health. Some species only survive in pristine waters whereas others thrive in nutrient-rich water. Changes in the dominant species may indicate a change in water quality and/or streambed composition. The Family Biotic Index (FBI) is a sum of the number of individuals in a family times a tolerance factor, divided by the total number of individuals. Tolerance scales range from 10 to 0 with 10 indicating poor condition. This measure can be used to indicate stream health or changes in water quality. Additional indices also can be used.
Metrics	Metrics are groupings used for comparisons between the various taxa found at a site. For example, composition metrics generally are percentages of selected taxa or groups of taxa compared to the total number of individuals, and depending on the taxa, increase or decrease with stream health. Feeding measures represent the percentage of the macroinvertebrates that feed in a particular way and also provide some indication of the health of the stream or changes in the stream reach.
<i>Water Supply</i>	
Groundwater dynamics	Changes in ground-water levels are indicators of climatic cycles/changes as well as changes in land use and water-management practices. For example, over use of an aquifer near the park may result in a decreased ground-water supply within the park. Spring flow may also decline as the result of over use of an aquifer.
Lake/impoundment dynamics	Lake and impoundment levels are indicators of many of the same changes as are noted in stream flow. In addition, impoundment levels may provide insight into response to management practices for grazing or wildlife use and hydrogeologic conditions of the impoundment.
Stream dynamics	Changes in stream flow discharge, levels, and velocity are indicators of changes in water use, water management, and short- and long-term climatic changes. Changes also may be related to other impacts, such as declines in stream riparian cover or impacts from invasive plant species.

Table B.7. Potential indicators and measures for NGPN aquatic resources (continued).

Indicator / Measures	Description of information provided by measures
<i>Stream sediment and geomorphology</i>	
Bank characteristics	The measured rate of stream bank erosion may be an indicator of increasing flow and may result in changes in the shape, sinuosity, gradient, and hydraulic geometry of a river. Changes in the geomorphology of banks may affect aquatic organisms, riparian conditions, and influence invasive plant species. Bank erosion also may pose a threat to natural or man-made elements that are of aesthetic or cultural concern.
Bed characteristics	Measurement of downcutting and scouring are indicators that the flow dynamics and hydraulic geomorphology of a stream/river have changed. Organisms within the aquatic system may be affected by changes in depth, shape, and slope of the stream bed.
Sediment properties	Sediment transport is common NGPN streams and may be an indicator of changes in streams and rivers. The hydrodynamics and sediment load may be affected by natural factors such as decreasing/increasing rainfall and the geological and climatic character of the drainage basin, or by anthropogenic factors such as land use and man-made structures. Sampling of sediments within the water column and on the stream bed can measure sediment concentration, particle size, and substrate composition that may affect the aquatic system.

Implications of Conceptual Models for NGPN Vital Signs and Protocols

Implications of General Model for NGPN Vital Signs and Protocols

A primary purpose of the NGPN general conceptual model was to categorize and provide a context for discussing major influences on NGPN systems. Developing this section cemented the importance of Weather and Climate as a Vital Sign, reinforced our need for accessing weather/climate data relevant to each Network park, and provoked initial discussions about which climatic variables we will need for integration into vegetation monitoring analyses, and at what spatial/temporal scales. Reviewing the importance of hydrology and ecologically dominant species in the NGPN for this and other conceptual models clarified the need for accessing and reporting data on existing monitoring of stream flow from USGS and state gages, for accessing monitoring data on groundwater level from state, resource conservation district, and park monitoring, and for accessing data on ungulate and prairie dog relative abundances from park monitoring. As a result, Surface Water Dynamics, Groundwater Dynamics, and Ungulates were incorporated as NGPN Vital Signs that depend largely on data collected by other monitoring efforts without I&M funding. Based on consideration of the role of prairie dogs in NGPN grasslands, we expanded the Prairie Dog Vital Sign to cover all five NGPN parks where this species is present; monitoring will be conducted through a combination of NGPN park and core I&M funding.

General Stressor Model

This model and its narrative led us to clarify which NGPN Vital Signs are selected specifically because they address potentially important stressors in the Network: (four air quality Vital Signs, Aquatic Contaminants, Aquatic Microorganisms, Exotic Plant Early Detection, Visitor Use, and Soundscape). Prior to development of this model, the NGPN had focused on funding additional ozone monitoring as a key air quality stressor; however, the modeling effort led to discussions about the relative threats posed by ozone, nitrogen deposition, and mercury. As a result, the Network decided to collaborate with NPS Air Resources Division and a researcher at the South Dakota School of Mines and Technology on additional preliminary work and discussions to determine which, if any, of these stressors pose major ecological threats to NGPN ecosystems. Developing this model also prompted further thought about management actions that by definition are stressors and that influence vegetation composition and structure (Treatments of Exotic Infestations, and fuels-treatments components of Fire and Fuel Dynamics).

Conceptual Diagrams

These models were developed after NGPN Vital Signs were finalized. However, discussions with these four parks reinforced the importance of Surface Water Dynamics, Groundwater Dynamics, Stream and River Channel Characteristics, water quality attributes, Soundscape, Viewscape, Visitor Use, and Land Cover and Use as Vital Signs to be monitored with I&M funding or for which data will be accessed from existing monitoring efforts. These diagrams reinforced the need for developing conceptual models that help integrate monitoring, data analysis, and reporting across multiple Vital Signs, although such integrative models have not yet been developed. Similarly, the need for developing conceptual models for landscape pattern

and dynamics (or adopting models developed by other Networks) was reinforced as an important first step to be taken in developing the Landscape Pattern and Dynamics protocol.

Grassland Models

These models helped the NGPN prioritize vegetation composition as a top monitoring priority and reinforced the need for accessing data on ungulates, prairie dogs, and prescribed and uncontrolled fires into analysis of vegetation monitoring data. As with the general ecological model, development of this section was a factor leading us to incorporate Ungulates and Fire and Fuel Dynamics as Vital Signs addressed mainly with data collected from parks and other programs. Based on consideration of nutrient dynamics in NGPN systems, the Network discussed cost-effective, feasible measures of critical nutrient-related processes in our terrestrial systems (related to the Nutrient Dynamics model), but did not select any related Vital Signs; the opportunity to add such monitoring at vegetation-monitoring sites will be re-examined once the Plant Communities Protocol is in operation.

State-transition Models

The primary intent of these models was to increase our understanding of NGPN vegetation dynamics and terrestrial vegetation types. However, developing these models affected our list of proposed Vital Signs and planned monitoring measures in several ways: First, these models reinforced the importance of fire in all NGPN terrestrial systems, but especially the management importance of fire suppression, increased tree densities, and increase vulnerability to insect outbreaks in Black Hills forests. As a result, the NGPN Plant Communities protocol added a proposed monitoring component focusing on extensive measures of tree and selected tall shrub density and composition in Black Hills parks.

Second, although floodplain woodland models are not fully developed, initial literature review for these sites indicated that loss of floodplain tree recruitment due to dam-caused cessation of flooding is a critical issue in the NGPN. The Network's grassland parks incorporate floodplain woodlands ranging from highly degraded sites succeeding into shrublands and grasslands to relatively healthy sites in which floods and regeneration still occur. This review led the Network to propose adding tree and tall shrub measurements in extensive woody vegetation plots in floodplains of selected NGPN parks. This also reinforced the need for accessing hydrology data as part of the Surface Water and Groundwater Dynamics Vital Signs.

Third, these models reinforced the need for incorporating Vital Signs that access data from existing monitoring efforts relevant to grazing (Ungulates and Prairie Dogs), fire (Fire and Fuels Dynamics), and other disturbances (Forest Insects and Diseases, Treatments of Exotic Infestations, Extreme Disturbances). Finally, consideration of these models has provoked thought about how the Plant Communities Protocol will be integrated with the Landscape Pattern and Dynamics protocol to provide a more complete examination of changes in vegetation composition and structure. In particular, many changes in gross vegetation structure at large

scales can be monitored with remote sensing; integration of these efforts will be discussed as the Landscapes protocol is developed.

Invasive Model

Development of this model reinforced the importance of Exotic Early Detection as a NGPN Vital Sign and the importance of exotic species as a primary stressor of Network ecosystems.

Vertebrate Models

These models helped the NGPN prioritize Ungulates and to a lesser extent, Landbirds and Raptors, as Vital Signs. Development of the prairie dog model reinforced the ecological importance of this species in NGPN grasslands. This model reinforced the importance of tracking the spatial extent of this species at all five NGPN parks where it is present, provoking discussion about the feasibility of a protocol integrating park-specific monitoring with I&M data management and reporting. Development of this model led to initial discussions about possibilities of integrating prairie dog monitoring with some vegetation measurements and monitoring of birds and other species dependent on prairie dog colonies.

Cave Models

Wind Cave and Jewel Cave park cave specialists had focused on water quality, water quantity, and meteorology as top monitoring priorities before model development. However, developing these models clarified the Network's justification for focusing on Cave Water, Cave Meteorology, and aquifer water level in Wind Cave (as part of the Groundwater Dynamics Vital Sign) in contrast to biotic or other abiotic attributes. Discussions held as part of model development helped the Network develop more specific and feasible draft monitoring objectives for the Cave Water and Meteorology Protocol; the information transfer from cave specialists to I&M core staff has helped the Network define its target population for this protocol (e.g., focusing on accessible areas because of the cost and potential impact of accessing random sites in the cave) and will help I&M core staff provide more specific input about the strengths and limitations of proposed monitoring designs. Discussions with NGPN cave specialists about links between the cave system with other surface and groundwater influences inside and outside the two cave parks reinforces the need for further consideration of how cave Vital Signs can be linked with monitoring of landscape characteristics, groundwater dynamics, visitor use, vegetation composition, and other attributes.

Aquatic Models

Compilation of these models helped reinforce the importance of Stream and River Channel Characteristics, Surface Water Dynamics, and Groundwater Dynamics as Vital Signs that would be monitored mainly through existing efforts. Aquatic models formed the basis for initial prioritizations about which monitoring measures were top priorities in each NGPN park, and in which water bodies. Listing general measures that could be taken for various indicators has demonstrated the need for more detailed submodels and consideration of specific properties that can be summarized and analyzed, particularly for stream/river flow data.

Literature Cited

- Abrams, M. D. 1986. Historical development of gallery forests in northeast Kansas. *Vegetation* **65**:29–37.
- Agnew, W. 1983. Flora and fauna associated with prairie dog ecosystems. Thesis. Colorado State University, Fort Collins, CO.
- Agnew, W., D. W. Uresk, and R. M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. *Journal of Range Management* **39**:135–13.
- Agnew, W., D. W. Uresk, and R. M. Hansen. 1988. Arthropod consumption by small mammals on prairie dog colonies and adjacent un-grazed in western South Dakota. Pages 81–87 in D. W. Uresk, G. L. Schenbeck, and R. Cefkin, technical editors. Eighth Great Plains Wildlife Damage Control Workshop Proceedings, Rapid City, SD, April 1987. General Technical Report RM-154. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Ahler, S. A., T. D. Thiessen, and M. K. Trimble. 1991. People of the willows: the prehistory and early history of the Hidatsa Indians. University of North Dakota Press, Grand Forks.
- Albertson, F. W., and J. E. Weaver. 1945. Injury and death or recovery of trees in prairie climate. *Ecological Monographs* **15**:393–433.
- Albertson, F. W., and J. E. Weaver. 1946. Reduction of ungrazed mixed prairie to short grass as a result of drought and dust. *Ecological Monographs* **16**:449–463.
- Albertson, F. W., G. W. Tomanek, and A. Riegel. 1957. Ecology of drought cycles and grazing intensity on grasslands of central Great Plains. *Ecological Monographs* **27**:27–44.
- Albertson, F. W. and G. W. Tomanek. 1965. Vegetation changes during a thirty-year period in grassland communities near Hayes, Kansas. *Ecology* **46**:714–720.
- Allen, K. K. 2003. Evaluation of MPB activity on the Black Hills National Forest. Biological Evaluation R2-04-02. U.S. Forest Service, Rocky Mountain Region, Renewable Resources. Online. (http://www.fs.fed.us/r2/fhm/reports/be_r2-04-02.pdf). Accessed 24 April 2009.
- Allen, T. F. H. and T. W. Hoekstra. 1992. Toward a unified ecology. Columbia University Press, New York, NY.
- Anderson, G. L., J. H. Everitt, D. E. Escobar, N. R. Spencer, and R. J. Andrascik. 1996. Mapping leafy spurge (*Euphorbia esula*) infestations using aerial photography and geographic information systems. *Geocarto International* **11**:81–89.
- Anderson, R. C. 1982. An evolutionary model summarizing the roles of fire, climate and grazing animals in the origin and maintenance of grasslands. Pages 297–308 in J. R. Estes, R. J. Tylr and J. N. Brunken, editors. Grasses and grasslands: systematics and ecology. University of Oklahoma Press, Norman, OK.
- Anderson, R. C. 1990. The historic role of fire in the North American grassland. Pages 8–18 in S. L. Collins and L. L. Wallace, editors. Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, OK.
- Axelrod, D. I. 1985. Rise of the grassland biome, central North America. *Botanical Review* **51**:163–202.

- Bachelet, D., J. M. Lenihan, C. Daly, and R. P. Neilson. 2000. Interactions between fire, grazing and climate change at Wind Cave National Park, SD. *Ecological Modelling* **134**:229 – 244.
- Bailey, R. G. 1995. Descriptions of the ecoregions of the United States. U.S. Forest Service. Online. (www.fs.fed.us/land/ecosysmgmt/ecoreg1_home.html). Accessed 4 March 2005.
- Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* **34**:177–185.
- Bakker, J. D., and S. D. Wilson. 2004. Using ecological restoration to constrain biological invasion. *Journal of Applied Ecology* **41**:1058–1064.
- Bakker, J. P., and J. C. Ruyter. 1981. Effects of five years of grazing on a salt-water marsh. *Vegetatio* **44**:81–100.
- Bangert, R. K., and C. N. Slobodchikoff. 2000. The Gunnison's prairie dog structures a high desert grassland landscape as a keystone engineer. *Journal of Arid Environments* **46**:357–369.
- Barber, M. C., ed. 1994. Environmental monitoring and assessment program indicator development strategy. EPA/620/R-94/022. Environmental Protection Agency, Office of Research and Development, Environmental Research Laboratory. Athens, GA.
- Barns, S. M., M. N. Spilde, L. J. Crossey, P. J. Boston, D. O. Natvig, and C. N. Dahm. 2003. Diverse microbial communities inhabiting ferromanganese deposits in Lechuguilla and Spider Caves. *Environmental Microbiology* **5**:1071–1086.
- Barrett, G. W., G. M. Van Dyne, and E. P. Odum. 1976. Stress ecology. *BioScience* **26**:192–194.
- Beck, J. L. and D. L. Mitchell. 2000. Influences of livestock grazing on sage grouse habitat. *Wildlife Society Bulletin* **28**:993–1002.
- Benkobi, L. B. and D. W. Uresk. 1996. Seral stage classification and monitoring model for big sagebrush/western wheatgrass/blue grama habitat. Pages 69–73 in J. R. Barrow, E. D. McArthur, R. E. Sosebee, and R. J. Tausch, compilers. *Proceedings: shrubland ecosystem dynamics in a changing environment*. General Technical Report INT-GTR-338. U.S. Forest Service Intermountain Research Station, Odgen, UT.
- Birken, A.S., and D. J. Cooper. 2006. Processes of *Tamarix* invasion and floodplain development along the lower Green River, Utah. *Ecological Applications* **16**:1103–1120.
- Black, C. C. 1971. Ecological implications of dividing plants into groups with distinct photosynthetic production capacities. *Advances in Ecological Research* **7**:87–114.
- Blair, J. M., T. R. Seastedt, C. W. Rice, and R. Ramundo. 1998. Terrestrial nutrient cycling in tallgrass prairie. Pages 222–243 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, NY.
- Boldt, C. E., R. R. Alexander, and M. J. Larson. 1983. Interior ponderosa pine in the Black Hills. Pages 80–83 in *Silvicultural systems for the major forest types of the United States*. Agricultural Handbook 445. U.S. Department of Agriculture, Washington, D. C.
- Boldt, C. E., D. W. Uresk, and K. E. Severson. 1978. Riparian woodlands in jeopardy on the northern High Plains. Pages 184–189 in R. R. Johnson and J. F. McCormick, editors. *Proceedings of a national symposium on strategies for protection and management of flood-plain wetlands and other riparian ecosystems*. General Technical Report WO-12. U.S. Forest Service, Washington, D.C.
- Borchert, J. R. 1950. The climate of the central North American grassland. *Annals of the Association of American Geographers* **40**:1–39.

- Bragg, T. B. 1982. Seasonal variations in fuel and fuel consumption by fires in a bluestem prairie. *Ecology* **63**:7–11.
- Bragg, T. B. 1995. The physical environment of Great Plains grasslands. Pages 49–81 *in* A. Joern and K. H. Keeler, editors. *The changing prairie: North American grasslands*. Oxford University Press, New York, NY.
- Branson, F. A., and R. F. Miller. 1981. Effects of increased precipitation and grazing management on northeastern Montana rangelands. *Journal of Range Management* **34**:3–10.
- Briske, D. D., S. D. Fuhlendorf and F. E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology and Management* **58**:1–10.
- Brockway, D., R. Gatewood, and R. Paris. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management* **65**:135–152.
- Brooks, M. L., C. M. D’Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* **54**:677–688.
- Brown, P. M. 2006. Climate effects on fire regimes and tree recruitment in Black Hills ponderosa pine forests. *Ecology* **87**:2500–2510.
- Brown, P. M., and B. Cook. 2006. Early settlement forest structure in Black Hills ponderosa pine forests. *Forest Ecology and Management* **223**:284–290.
- Brown, P. M., and C. H. Sieg. 1999. Historical variability in fire at the ponderosa pine - Northern Great Plains prairie ecotone, southeastern Black Hills, South Dakota. *EcoScience* **6**:539–547.
- Brown, P. M., C. L. Wienk, and A. J. Symstad. 2008. Fire and forest history at Mount Rushmore. *Ecological Applications* **18**:1984–1999.
- Brown, R. W. 1971. Distribution of plant communities in southeastern Montana badlands. *American Midland Naturalist* **85**:458–477.
- Bryson, R. A. and F. K. Hare, editors. 1974. *World survey of climatology. Volume 11, Climates of North America*. Elsevier Scientific Publishing, New York, NY.
- Burger, L. D., L. W. Burger, Jr., and J. Faaborg. 1994. Effects of prairie fragmentation on predation on artificial nests. *Journal of Wildlife Management* **58**:249–254.
- Burzlaff, D. F. 1962. A soil and vegetation inventory and analysis of three Nebraska Sandhills range sites. *Agricultural Experiment Station Research Bulletin* 206. University of Nebraska, College of Agriculture. Lincoln.
- Busch, E. D. and J. C. Trexler. 2003. The importance of monitoring in regional ecosystem initiatives. Pages 1–23 *in* E. D. Busch and J. C. Trexler, editors. *Monitoring ecosystems: interdisciplinary approaches for evaluating ecoregional initiatives*. Island Press, Washington, D.C.
- Butler, J. L., and D. R. Cogan. 2004. Leafy spurge effects on patterns of plant species richness. *Journal of Range Management* **57**:305–311.
- Butler, J. L., and M. A. Trammell. 1995. Final report: exotic plants of Theodore Roosevelt National Park: extent, distribution, and ecological impact. Unpublished report. Department of Biology, University of South Dakota, Vermillion.
- Cappock, D. L., J. Detling, E. Ellis and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal

- aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* **56**:1–9.
- Carter, J. M., D. G. Driscoll, J. E. Williamson, and V. A. Lindquist. 2002. Atlas of water resources in the Black Hills area, South Dakota. U. S. Geological Survey Hydrologic Investigations Atlas HA-747. U.S. Department of Interior, U.S. Geological Survey, Reston, VI.
- Catchpole, F. B. 1996. The dynamics of bison (*Bos bison*) grazing patches in tallgrass prairie. Thesis. Kansas State University, Manhattan.
- Chapin III, F. S., M. S. Torn, and M. Tateno. 1996. Principles of ecosystem sustainability. *American Naturalist* **148**:1016–1037.
- Chippendale, J. F. 1991. The potential returns to research into rubber vine (*Cryptostegia grandiflora*) in north Queensland. Thesis, University of Queensland, Australia.
- Christian, J. M., and S. D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the Northern Great Plains. *Ecology* **80**:2397–2407.
- Christiansen, E., R. Waring, and A. Berryman. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *Forest Ecology and Management*. **22**:89–106.
- Cid, M. S., J. K. Detling, A. D. Whicker, and M. A. Brizuela. 1991. Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. *Journal of Range Management* **44**:100–105.
- Cincotta, R. P., D. W. Uresk, and R. M. Hansen. 1988. A statistical model of expansion in a colony of black-tailed prairie dogs. Pages 30–33 in D. W. Uresk, G. L. Schenbeck, and R. Cefkin, technical editors. Eighth Great Plains Wildlife Damage Control Workshop Proceedings, Rapid City, SD, April 1987. General Technical Report RM-154. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Cincotta, R. P., D. W. Uresk, and R. M. Hansen. 1989. Plant compositional changes in a colony of black-tailed prairie dogs in South Dakota. Pages 171–177 in A. J. Bjugstad, D. W. Uresk, and R. H. Hamre, technical editors. Ninth Great Plains Wildlife Damage Control Workshop Proceedings, Fort Collins, CO, 1989. General Technical Report RM-171. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Clark, J. S., E. C. Grimm, J. J. Donovan, S. C. Fritz, D. R. Engstrom, and J. E. Almendinger. 2002. Drought cycles and landscape responses to past aridity on prairies of the Northern Great Plains. *Ecology* **83**:595–601.
- Cogan, D., H. Marriot, J. Von Loh and M. Pucherelli. 1999. USGS-NPS Vegetation Mapping Program, Wind Cave National Park, South Dakota.
- Coladonato, M. 1992. *Ulmus americana*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 4 May 2007.
- Collins, S. L. and L. L. Wallace, editors. 1990. Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, OK.
- Collins, S. L., and S. M. Glenn. 1995. Grassland ecosystem and landscape dynamics. Pages 128–156 in A. Joern and K. H. Keeler, editors. The changing prairie: North American Grasslands. Oxford University Press, New York, NY.
- Cook, J. G., and L. L. Irwin. 1992. Climate-vegetation relationships between the Great Plains and Great Basin. *American Midland Naturalist* **127**:316–326.
- Cook, R. R.; J. E. Cartron, and P. J. Polechla Jr. 2003. The importance of prairie dogs to nesting ferruginous hawks in grassland ecosystems. *Wildlife Society Bulletin* **31**:1073–1082.

- Coppedge, B. R., D. M. Engle, C. S. Toepfer, and J. H. Shaw. 1998. Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. *Plant Ecology* **139**:235–246.
- Coppedge, B. R., and J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. *Journal of Range Management* **51**:258–264.
- Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on inter-seasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* **56**:1–9.
- Coppock, D. L. and J. K. Detling. 1986. Alteration of bison/prairie dog grazing interaction by prescribed burning. *Journal of Wildlife Management* **50**:452–455.
- Coupland, R.T. 1992. Mixed prairie. Pp. 151–182 in R.T. Coupland, editor. *Ecosystems of the world: natural grasslands*. Elsevier. Amsterdam.
- Dale, V. H., S. Brown, R. A. Haeuber, N. T. Hobbs, N. Huntly, R. J. Naiman, W. E. Riebsame, M. G. Turner, and T. J. Valone. 2000. Ecological principles and guidelines for managing the use of land. *Ecological Applications* **10**:639–670.
- Day, T. A. and J. K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* **63**:180–188.
- Debano, L. F., D. G. Neary, and P. F. Folliot. 1998. *Fire's effects on ecosystems*. John Wiley and Sons, Inc., New York.
- Deisch, M. S., D. W. Uresk and R. L. Linder. 1990. Effects of prairie dog rodenticides on deer mice in western South Dakota. *Great Basin Naturalist* **50**:347–353.
- Dennison, W. C., T. R. Lookingbill, T. J. B. Carruthers, J. M. Hawkey, and S. L. Carter. 2007. An eye-opening approach to developing and communicating integrated environmental assessments. *Frontiers in Ecology and the Environment* **5**:307–314.
- Desmond, M. J., J. A. Savidge, and T. F. Seibert. 1995. Spatial patterns of burrowing owl (*Speotyto cunicularia*) nests within black-tailed prairie dog (*Cynomys ludovicianus*) towns. *Canadian Journal of Zoology* **73**:1375–1379.
- Detling, J. K. 1998. Mammalian herbivores: ecosystem-level effects in two grassland national parks. *Wildlife Society Bulletin* **36**:438–448.
- Di Tomaso, J. M. 1998. Impact, biology, and ecology of saltcedar (*Tamarix* spp.) in the southwestern United States. *Weed Technology* **12**:326–336.
- Dodds, W.K., R.E. Hutson, A.C. Eichern, M.A. Evans, D.A. Gudder, K.M. Fritz, and L. Gray. 1996. The relationship of floods, drying, flow and light to primary production and producer biomass in a prairie stream. *Hydrobiologia* **333**:151–159.
- Dyer, M. I., J. K. Detling, D. C. Coleman, and D. W. Hilbert. 1982. The role of herbivores in grassland. Pages 225–261 in J. R. Estes, R. J. Tylr, and J. N. Bunken, editors. *Grasses and Grasslands*. University of Oklahoma Press, Norman, Oklahoma, OK.
- Earl, S. R., and D. W. Blinn. 2003. Effects of wildfire ash on water chemistry and biota in Southwestern U.S.A. streams. *Freshwater Biology* **48**:1015–1030.
- Engle, D. M., S. D. Fuhlendorf, and B. R. Coppedge. 2003. Conservation priorities on fragmented, homogenized, Great Plains landscapes. Pages 1–6 in S. Fore, editor. *Proceedings of the 18th North American Prairie Conference: Promoting Prairie*. Truman State University, Kirksville, MO.

- Evans, K. E. and G. E. Probasco. 1977. Wildlife of the prairies and plains. General Technical Report NC-29. U.S. Forest Service, North Central Forest Experiment Station, St. Paul, MN.
- Fahnestock, J. T. and A. K. Knapp. 1993. Water relations and growth of tallgrass prairie forbs in response to selective grass herbivory and water stress. *International Journal of Plant Science* **154**:123–131.
- Fahnestock, J. T. and A. K. Knapp. 1994. Plant responses to selective grazing by bison: interactions between light, herbivory and water stress. *Vegetation* **115**:123–131.
- Fannin, T. E., and B. J. Esmoil. 1993. Metal and organic residues in addled eggs of least terns and piping plovers in the Platte Valley of Nebraska. Pages 150–158 in K. F. Higgins and M. R. Brashier, editors. *Proceedings, the Missouri River and its tributaries: piping plover and least tern symposium/workshop*. South Dakota State University, Brookings.
- Fedkiw, J. 1989. The evolving use and management of the Nation's forests, grasslands, croplands, and related resources. General Technical Report RM-175. U.S. Forest Service, Washington, D.C.
- Fisher, R. F., M. J. Jenkins, and W. F. Fisher. 1987. Fire and the prairie-forest mosaic of Devils Tower National Monument. *American Midland Naturalist* **117**:250–257.
- Foran, B.D. & G. Bastin. 1984. The dynamics of Mitchell grass rangeland on the Barkly tableland, Northern Territory. *Australian Rangeland Journal* **6**:92–97.
- Frank, A. B., and J. F. Karn. 2005. Shrub effects on carbon dioxide and water vapor fluxes over grasslands. *Rangeland Ecology and Management* **58**:20–26.
- Frank, D. A., R. S. Innoye, N. Huntly, G. W. Minshall, and J. E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. *Biogeochemistry* **26**:163–188.
- Frank, D. A. and R. D. Evans. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. *Oecologia* **96**:157–161.
- Frank, D. A. and S. J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oecologia* **96**:157–161.
- Frank, D. A. and Y. Zhang. 1997. Ammonia volatilization from a seasonally and spatially variable grazed grassland: Yellowstone National Park. *Oecologia* **36**:189–203.
- French, N. R., W. E. Grant, W. Grodzinski, and D. M. Smith. 1976. Small mammal energetics in grassland ecosystems. *Ecological Monographs* **46**:201–220.
- Friedman, J. M., M. L. Scott, and G. T. Auble. 1997. Water management and cottonwood forest dynamics along prairie streams. Pages 49–71 in F. L. Knopf and F. B. Samson, editors. *Ecology and conservation of Great Plains vertebrates*. Springer-Verlag, New York, NY.
- Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* **51**:625–632.
- Fuhlendorf, S. D. and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology* **41**:604–614.
- Fuls, E.R. 1992. Semi-arid and arid rangelands: a resource under siege due to patch-selective grazing. *Journal of Arid Environments* **22**:191–193.
- Gibson, D. J., and L. C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tall-grass prairie. *Vegetatio* **72**:175–182.
- Gillen, R. L., and P. L. Sims. 2006. Stocking rate and weather impacts on sand sagebrush and grasses: a 20-year record. *Rangeland Ecology and Management* **59**:145–152.

- Girard, M. M., H. Goetz, and A. J. Bjugstad. 1987. Factors influencing woodlands of southwestern North Dakota. *Prairie Naturalist* **19**:189–198.
- Girard, M. M., H. Goetz, and A. J. Bjugstad. 1989. Native woodland habitat types of southwestern North Dakota. Research Paper RM-281. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Gordon, N. D., T. A. McHahon, B. L. Finlayson. 1992. Stream hydrology: an introduction for ecologists. John Wiley and Sons Inc., New York, NY.
- Grace, J. B., M. D. Smith, S. L. Grace, S. L. Collins, and T. J. Stohlgren. 2001. Interactions between fire and invasive plants in temperate grasslands in North America. Pages 40–65 in K.E.M. Galley and T.P. Wilson, editors. Proceedings of the invasive species workshop: The role of fire in the control and spread of invasive species. Fire Conference 2000: The First National Congress on Fire Ecology, Prevention, and Management. Tall Timbers Research Station, Tallahassee, FL.
- Grafe, E., and P., Horsted. 2002. Exploring with Custer: The 1874 Black Hills Expedition. Golden Valley Press, Custer, SD.
- Grant, T. A., E. Madden, and G. B. Berkey. 2004. Tree and shrub invasion in northern mixed-grass prairie: implications for breeding grassland birds. *Wildlife Society Bulletin* **32**:807–818.
- Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* **9**:399–409.
- Gray, L. J., and W. K. Dodds. 1998. Structure and dynamics of aquatic communities. Pages 177–189 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, NY.
- Gray, L. J., G. L. Macpherson, J. K. Koelliker, and W. K. Dodds. 1998. Hydrology and aquatic chemistry. Pages 1159–176 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, NY.
- Green, R. A. and J. K. Detling. 2000. Defoliation-induced enhancement of total aboveground nitrogen yield of grasses. *Oikos* **91**:280–284.
- Groffman, P. M., C. W. Rice, and J. M. Tiedje. 1993. Denitrification in a tallgrass prairie. *Ecology* **74**:855–862.
- Gucker, Corey L. 2005. *Fraxinus pennsylvanica*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 5 May 2007.
- Gucker, C. L. 2006. *Juniperus horizontalis*. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 21 February 2007.
- Guijarro, J. A. 2006. Package ‘climatol’: some tools for climatology. [User’s guide and software available.] Online. (<http://webs.ono.com/climatol/climatol.html>). Accessed 15 January 2007.
- Hagle, S. K., K. E. Gibson, and S. Tunnock. 2003. A field guide to diseases & insect pests of Northern & Central Rocky Mountain conifers. U.S. Forest Service State and Private Forestry, Northern Region, and Intermountain Region. Online. (http://www.fs.fed.us/r1-r4/spf/fhp/field_guide/index.htm) Accessed 24 April 2009.
- Hansen, P. L., G. R. Hoffman, and A. J. Bjugstad. 1984. The vegetation of Theodore Roosevelt National Park, North Dakota: a habitat type classification. General Technical Report RM-

113. U.S. Forest Service, Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO.
- Hanson, H. C., and W. Whitman. 1938. Characteristics of major grassland types in western North Dakota. *Ecological Monographs* **8**:57–114
- Harrod R. J., and S. Reichard. 2001. Fire and invasive species within the temperate and boreal coniferous forests of western North America. Pages 95–101 in K. E. M. Galley and T. P. Wilson, Eds. *Proceedings of the Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species*. Fire Conference 2000: The First National Congress on Fire Ecology, Prevention, and Management. Tall Timbers Research Station, Tallahassee, FL.
- Hart, R. H., and J. A. Hart. 1997. Rangelands of the Great Plains before European settlement. *Rangelands* **19**:4–11.
- Hartnett, D.C. and P.A. Fay. 1998. Plant populations: Patterns and processes. Pages 81–100 in A.K. Knapp, J.M. Briggs, D.C. Martnett, and S.L. Collins, eds. *Grassland dynamics: Long-term ecological research in tallgrass prairie*. Oxford University Press, New York, NY.
- Hauser, A. S. 2006. *Carex filifolia*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 30 May 2006.
- Hazlett, D. L., and G. R. Hoffman. 1975. Plant species distributional patterns in *Artemisia tridentata* and *Artemisia cana* dominated vegetation in western North Dakota. *Botanical Gazette* **136**:72–77.
- Herkert, J. R. 1994. The influence of habitat fragmentation on Midwestern grassland bird communities. *Ecological Applications* **4**:461–471.
- Hesse, L. W., and W. Sheets. 1993. The Missouri River hydrosystem. *Fisheries* **18**:5–14.
- Hester, F. E. 1991. The U.S. National Park Service experience with exotic species. *Natural Areas Journal* **11**:127–128.
- Hinckley, D. 1995. Great Plains climates and biota: past, present, and future. Pages 149–159 in S. R. Johnson, and A. Bouzaher, editors. *Conservation of Great Plains ecosystems: current science, future options*. Kluwer Academic, New York, NY.
- Higgins, K. F., A. D. Kruse, and J. L. Piehl. 1989. Effects of fire in the Northern Great Plains. Extension Circular 761. U.S. Fish and Wildlife Service and Cooperative Extension Service, South Dakota State University, Brookings, SD. Online. (<http://www.npwrc.usgs.gov/resource/habitat/fire/index.htm>). Accessed 20 February 2007.
- High Plains Regional Climate Center (HPRCC). 2007. High Plains Regional Climate Center, University of Nebraska, Lincoln. Online. (<http://www.hprcc.unl.edu/index.php>). Accessed 27 November 2007.
- Hobbs, R. J., D. S. Schimel, C. E. Owensby, and D. S. Ojima. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* **72**:1374–1382
- Hodorff, R. A., and C. H. Sieg. 1986. Bird species associated with green ash woodlands in the Slim Buttes, South Dakota. *South Dakota Bird Notes* **38**:56–60.
- Hodorff, R. A., C. H. Sieg, and R. L. Linder. 1988. Wildlife response to stand structure of deciduous woodlands. *Journal of Wildlife Management* **52**:667–673.
- Holland, E. A. and J. K. Detling. 1990. Plant response to herbivory and belowground nutrient cycling. *Ecology* **71**:1040–1049.

- Hoogland, J. L. 2006. Conservation of the black-tailed prairie dog: saving North America's western grasslands. Island Press, Washington, D.C.
- Howard, J. L. 1999. *Artemisia tridentata* subsp. *wyomingensis*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 28 March 2008.
- Howard, J. L. 2002. *Artemisia cana*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 27 April 2007.
- Hubbell S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.
- Irby, L. R., J. E. Norland, M. G. Sullivan, J. A. Westfall, Jr., and P. Andersen. 2000. Dynamics of green ash woodlands in Theodore Roosevelt National Park. *Prairie Naturalist* **32**:76–102.
- James, S. W. 1991. Soil, nitrogen, phosphorus, and organic matter processing by earthworms in tall-grass prairie. *Ecology* **72**:2101–2109.
- Jaramillo, W. J. and J. K. Detling. 1988. Grazing history, defoliation, and competition: effects on shortgrass production and nitrogen accumulation. *Ecology* **69**:1599–1608.
- Jenny, H. 1941. Factors of soil formation: a system of quantitative pedology. McGraw-Hill, New York, NY.
- Jensen, W. F. 1992. Mule deer habitat use in the North Dakota Badlands. *Prairie Naturalist* **24**:97–108.
- Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment* **5**:365–374.
- Johnsgard, P. A. 2005. *Prairie dog empire: a saga of the shortgrass prairie*. University of Nebraska Press, Lincoln.
- Johnson, W. C. 1992. Dams and riparian forests: case study from the Upper Missouri River. *Rivers* **3**:229–242.
- Kantak, G. E. 1995. Terrestrial plant communities of the middle Niobrara valley, Nebraska. *Southwestern Naturalist* **40**:129–138.
- Karr, J. R. 1991. Biological integrity: a long neglected aspect of water resources management. *Ecological Applications* **1**:66–84.
- Katz, G. L., and P. B. Shafroth. 2003. Biology, ecology, and management of *Elaeagnus angustifolia* L. (Russian olive) in western North America. *Wetlands* **23**:763–777.
- Kaufman, G. A. and D. W. Kaufman. 1997. Ecology of small mammals in prairie landscape. Pages 207–243 in Knopf, F. L. and F. B. Samson, editors. *Ecology and conservation of Great Plains vertebrates*. Springer, New York, NY.
- Kelly, Erin N., David W. Schindler, Vincent L. St. Louis, David B. Donald, and Katherine E. Vladicka. 2006. Forest fire increases mercury accumulation by fishes via food web restructuring and increased mercury inputs. *Proceedings of the National Academy of Sciences U.S.A.* **103**:19380–19385.
- Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. *Bioscience* **49**:39–50.
- Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* **36**:662–69.

- Knight, D. H. 1994. Mountains and plains: the ecology of Wyoming landscapes. Yale University Press, New Haven, CT.
- Knopf, F. L. 1986. Changing landscapes and the cosmopolitan of the eastern Colorado avifauna. *Wildlife Society Bulletin* **14**:132–142.
- Knopf, F. L. 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* **15**:247–57.
- Knopf, F. L. 1996. Prairie legacies-birds. Pages 135–148 *in* F. B. Samson and F. L. Knopf, editors. *Prairie conservation: preserving North America's most endangered ecosystem*. Island Press, Covelo, CA.
- Knopf, F. L., and F. B. Samson. 1996. Conserving the biotic integrity of the Great Plains. Pages 121–134 *in* S. R. Johnson and A. Bouzaher, editors. *Conservation of the Great Plains ecosystems*. Kluwer, Boston.
- Knowles, C. J. 1986. Some relationships of black-tailed prairie dogs to livestock grazing. *Great Basin Naturalist* **46**:198–203.
- Knowles, C. J., C. J. Stoner, and S. P. Gieb. 1982. Selective use of black-tailed prairie dog towns by mountain plovers. *Condor* **84**:71–74.
- Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. *Wildlife Monographs* No. 3.
- Kotliar, N. B., B. W. Baker, A. D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. *Environmental Management* **24**:177–192.
- Kotliar, N. B. 2000. Application of the new keystone-concept to prairie dogs: how well does it work? *Conservation Biology* **14**:1715–1721.
- Kreuger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. *Ecology* **67**:760–770.
- Krueger-Mangold, J., R. L. Sheley, and B. D. Roos. 2002. Maintaining plant community diversity in a waterfowl production area by controlling Canada thistle (*Cirsium arvense*) using glyphosate. *Weed Technology* **16**:457–463.
- Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. American Geographical Society Special Publication Number 36.
- Kudray, G., and S. V. Cooper. 2005. Linking the National Vegetation Classification System to NRCS Ecological Sites in southeastern Montana. Report to the Bureau of Land Management. Montana Natural Heritage Program, Helena, MT.
- LANDFIRE. 2005a. Rapid assessment reference condition model. R0SBWYwy. Wyoming big sagebrush. U.S. Forest Service and U.S. Department of the Interior Landscape Fire and Resource Management Planning Tools Project. Online. (<http://www.landfire.gov/zip/NCR/R0SBWYwy.pdf>). Accessed 28 March 2007.
- LANDFIRE. 2005b. Rapid assessment reference condition model. R4WODR. Northern Great Plains wooded draws and ravines. U.S. Forest Service and U.S. Department of the Interior Landscape Fire and Resource Management Planning Tools Project. Online. (<http://www.landfire.gov/zip/NP/R4WODR.pdf>). Accessed 28 April 2007.
- Landsberg, J., C. D. James, S. R. Morton, W. J. Muller, and J. Stol. 2003. Trends in abundance and composition of plant species along grazing gradients in Australian rangelands. *Journal of Applied Ecology* **40**:1025–1034.
- Larson, D. L., P. J. Anderson, and W. Newton. 2001. Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. *Ecological Applications* **11**:128–141.

- Lauenroth, W. K. and D. G. Milchunas. 1992. Short-grass steppe. Pages 183–226 in R. T. Coupland, editor. *Ecosystems of the world 8A: natural grasslands: introduction and Western Hemisphere*. Elsevier, New York, NY.
- Lentile, L. B., F. W. Smith, and W. D. Shepperd. 2005. Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. *Canadian Journal of Forest Research* **35**:2875–2885.
- Lesica, P. 1989. The vegetation and condition of upland hardwood forests in eastern Montana. *Proceedings of Montana Academy of Sciences* **49**:45–62.
- Lesica, P. 2001. Recruitment of *Fraxinus pennsylvanica* (Oleaceae) in eastern Montana woodlands. *Madroño* **48**:286–292.
- Lesica, P. 2003. Effects of wildfire on recruitment of *Fraxinus pennsylvanica* in eastern Montana woodlands. *American Midland Naturalist* **149**:258–267.
- Lesica, P., H. E. Atthowe, and F. M. Dugan. 2003. Incidence of *Perenniporia fraxinophila* and its effects on green ash (*Fraxinus pennsylvanica*) woodlands in eastern Montana, USA. *Forest Ecology and Management* **182**:153–159.
- Lewis, H. T. 1973. Patterns of Indian burning in California. Ecology and ethnohistory. Ballena Press Anthropological Papers No. 1. Ballena Press, Menlo Park, CA.
- Lewis, M. 1961. The Lewis and Clark expedition. Volume 1. J. B. Lippincott, Philadelphia, PA.
- Licht, D. S. 1997a. Ecology and economics of the Great Plains. University of Nebraska Press, Lincoln.
- Licht, D. S. 1997b. The vanished wolves of the Great Plains. *International Wolf* **7**:3-6.
- Licht, D. S., and K. M. Johnson. 1992. Black-billed magpie predation on piping plover eggs. *Prairie Naturalist* **24**:285.
- Lomolino, M. V., and G. A. Smith. 2004. Terrestrial vertebrate communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns. *Biological Conservation* **115**:89–100.
- Longo, P. J., and D. W. Yoskowitz. 2002. Water on the Great Plains: issues and policies. Texas Tech University, Lubbock.
- Luckey, R. R., E. D. Gutentag, F. J. Heimes, and J. B. Weeks. 1988. Effects of future ground-water pumpage on the High Plains aquifer in parts of Colorado, Kansas, Nebraska, New Mexico, Oklahoma, South Dakota, Texas, and Wyoming. Professional Paper, 1400-E. U.S. Department of Interior, U.S. Geological Survey, Washington, D.C.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.
- Maddox, D., K. Poiani, and R. Unnasch. 1999. Evaluating management success: using ecological models to ask the right monitoring questions. Pages 563–584 in W. T. Sexton, A. J. Malk, R. C. Szaro, and N. C. Johnson, editors. *Ecological stewardship: a common reference for ecosystem management*. Vol. III. Elsevier Science, Oxford, UK.
- Marriott, H. J., and D. Faber-Langendoen. 2000. Black Hills community inventory, volume 2: plant community descriptions. The Nature Conservancy, Midwest Conservation Science Center and Association for Biodiversity Information, Minneapolis, MN.
- Martin, B., S. Cooper, B. Heidel, T. Hildebrand, G. Jones, D. Lenz, and P. Lesica. 1998. Natural community inventory within landscapes in the Northern Great Plains Steppe Ecoregion of the United States. A report to the Natural Resource Conservation Service, Northern Plains Regional Office. The Nature Conservancy, Helena, MT.
- Martin, S.C. and D. E. Ward. 1970. Rotating access to water to improve semi-desert cattle range near water. *Journal of Range Management* **23**:22–26.

- Marvin-DiPasquale, M., M. A. Lutz, M. E. Brigham, D. P. Krabbenhoft, G. R. Aiken, W. H. Orem, and B. D. Hall. 2009. Mercury cycling in stream ecosystems. 2. Benthic methylmercury production and bed sediment – pore water partitioning. *Environmental Science and Technology* **43**:2733–2739.
- Mattes, J. J. 1969. *The Great Platte River Road*. Vol. XXV, Nebraska State Historical Society, Lincoln.
- Matthews, W. J. 1988. North American prairie streams as systems for ecological study. *Journal of the North American Benthological Society* **7**:387–409.
- McBride, J. 1973. Natural replacement of disease-killed elms. *American Midland Naturalist* **90**:300–306.
- McCambridge, W. F., F. G. Hawksworth, C. B. Edminster, and J. G. Laut. 1982. Ponderosa Pine Mortality Resulting from a MPB Outbreak. Research Paper RM-235. U. S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. *BioScience* **38**:794–800.
- McNaughton, S. J. 1979. Grassland-herbivore dynamics. Pages 46–81 in A. R. E. Sinclair and M. Norton-Griffiths, editors. *Serengeti: Dynamics of an ecosystem*. University of Chicago Press, Chicago.
- McNeeley, J. A. 2001. An introduction to human dimensions of invasive alien species. Pages 5–20 in J.A. McNeeley, editor. *The great reshuffling: human dimensions of invasive alien species*. IUCN, Gland, Switzerland and Cambridge, U.K.
- McWilliams, Jack 2003a. *Artemisia filifolia*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 17 May 2007.
- McWilliams, J. 2003b. *Artemisia frigida*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 26 February 2007.
- Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* **63**:327–366.
- Milchunas, D. G., O. E. Sala and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* **132**:87–106.
- Meagher, M. M. 1978. Bison. Pages 123–134 in J. L. Schmidt and D. L. Gilbert, editors. *Big game of North America*. Stackpole Books, Harrisburg, PA.
- Miller B., R. Reading, D. Biggins, J. Detling, S. Forrest, J. Hoogland, J. Javersak, S. Miller, J. Proctor, J. Truett, and D. Uresk. 2007. Prairie dogs: an ecological review and current biopolitics. *Journal of Wildlife Management* **71**:2801–2810.
- Miller, B., R. Reading, J. Hoogland, T. Clark, G. Ceballos, R. List, S. Forrest, L. Hanebury, P. Manzano, J. Pacheco, and D. Uresk. 2000. The role of prairie dogs as keystone species: a response to Stapp. *Conservation Biology* **14**:318–321.
- Mills, T. R., M. A. Rumble, and L. D. Flake. 2000. Habitat of birds in ponderosa pine and aspen/birch forest in the Black Hills, South Dakota. *Journal of Field Ornithology* **71**:187–206.
- Mock, C. J. 1991. Drought and precipitation fluctuations in the Great Plains during the late nineteenth century. *Great Plains Research* **1**:26–57.

- Monson, R. K., M. E. Rumpho, and G. E. Edwards. 1983. The influence of inorganic phosphate on photosynthesis in intact chloroplasts from *Mesembryanthemum crystallinum* L. plants exhibiting C3 photosynthesis or Crassulacean acid metabolism. *Planta* **159**:97–104.
- Moore, C. T. 1972. Man and fire in the central North American grassland 1535-1890: a documentary historical geography. Dissertation. University of California, Los Angeles.
- Montana Natural Heritage Program. Undated. Community field guide: silver sagebrush / western wheatgrass shrub prairie. Online.
(http://nhp.nris.state.mt.us/community/guide_report.asp?elcode=CEGL001556). Accessed 22 April 2007.
- National Assessment Synthesis Team. 2000. Climate change impacts on the United States: The potential consequences of climate variability and change. U.S. Global Research Program. Cambridge University Press, UK.
- National Energy Technology Laboratory (NETL). 2007a. 2007 Coal power plant database. U.S. Department of Energy. National Energy Technology Laboratory. Online
(<http://www.netl.doe.gov/energy-analyses/pubs/database/NETL%20CPPDB%202007%20-%20Public.xls>). Accessed 26 November 2007.
- National Energy Technology Laboratory (NETL). 2007b. Tracking new coal-fired power plants: coal's resurgence in electric power generation. U.S. Department of Energy. National Energy Technology Laboratory. Online (<http://www.netl.doe.gov/coal/refshelf/ncp.pdf>). Accessed 14 September 2007.
- National Park Service (NPS). 2005a. Northern Great Plains Exotic Plant Management Plan and Environmental Assessment. Unpublished report. U.S. Department of Interior, National Park Service, Northern Great Plains Parks.
- National Park Service (NPS). 2005b. Southern Plains Network (SOPN) Vital Signs Monitoring Plan: Phase 1 Appendices. U.S. Department of Interior, National Park Service, Fort Collins, CO.
- National Park Service (NPS). 2006. Northern Great Plains Exotic Plant Management Team 2006 Annual Report and 2002-2006 Summary. U.S. Department of the Interior, National Park Service, Medora, ND.
- National Park Service (NPS). 2008. Southern Plains Network vital signs monitoring plan. Natural Resource Report NPS/SOPN/NRR-2008/028. U.S. Department of Interior, National Park Service, Fort Collins, CO.
- National Research Council. 1995. Review of EPA's environmental monitoring and assessment program: overall evaluation. National Academy Press, Washington, D.C.
- Natural Resources Conservation Service (NRCS). 2004. Ecological site descriptions. Natural Resources Conservation Service. Online.
(<http://esis.sc.egov.usda.gov/Welcome/pgReportLocation.aspx?type=ESD>). Accessed 14 February 2007.
- Natural Resources Conservation Service (NRCS). 2007. Mixed sandy and silty tableland (MLRA 64): Ecological site descriptions. Natural Resources Conservation Service. Online.
(http://www.ne.nrcs.usda.gov/technical/ESD_MLRA64.html). Accessed 14 February 2007.
- Naylor, R.L. 2000. The economics of alien species invasions. Pages 241–259 in H.A. Mooney and R.J. Hobbs, editors. *Invasive species in a changing world*. Island Press, Washington, D.C.

- Nelson, J. R. 1961. Composition and structure of the principal woody vegetation types in the North Dakota Badlands. Thesis. North Dakota State University, Fargo.
- Nienstaedt, H., and J. C. Zasada. 1990. *Picea glauca* (Moench) Voss: white spruce. Page 204–226 in R. M. Burns and B. H. Honkala, technical coordinators. Silvics of North America. Volume 1. Conifers. Agriculture Handbook 654. U.S. Forest Service, Washington, D.C.
- Noble, D. L. 1990. *Juniperus scopulorum* Sarg.: Rocky Mountain juniper. Page 116–126 in R. M. Burns and B. H. Honkala, technical coordinators. Silvics of North America. Volume 1. Conifers. Agriculture Handbook 654. U.S. Forest Service, Washington, D.C.
- Noon, B. R. 2003. Conceptual issues in monitoring ecological resources. Pages 27–72 in D.E. Busch and J.C. Trexler, editors. Monitoring ecosystems: interdisciplinary approaches for evaluating ecoregional initiatives. Island Press, Washington, D.C.
- Noon, B. R., T. A. Spies, and M. G. Raphael. 1999. Conceptual basis for designing an effectiveness monitoring program. Pages 21–48 in B. S. Mulder, B. R. Noon, T. A. Spies, M. G. Raphael, C. J. Palmer, A. R. Olsen, G. H. Reeves, and H. H. Welsh, technical coordinators. The strategy and design of the effectiveness monitoring program for the Northwest Forest Plan. General Technical Report PNW-GTR-437. U.S. Forest Service, Portland, Oregon.
- Ohms, Marc J. 2004. The Status of Groundwater Lakes in Wind Cave, Wind Cave National Park, South Dakota. Abstract, Western South Dakota Hydrology Conference, Rapid City, SD.
- Ojima, D. S., W. J. Parton, D. S. Schimel and C. E. Owensby. 1990. Simulated impacts of annual burning on prairie ecosystems. Pages 118–132 in S.L. Collins and L.L. Wallace, editors. Fire in North American tallgrass prairies. University of Oklahoma Press, Norman.
- Omernick, J. M. 1987. Ecoregions of the conterminous United States. Annals of the Association of American Geographers **77**:118–125.
- Palmer, A.N. 2000. Speleogenesis of the Black Hills maze caves, South Dakota, USA. Pages 274–281 in A. Klimchouk, D. Ford, A. Palmer, and W. Dreybrodt, editors. Speleogenesis and evolution of karst aquifers. National Speleological Society, Inc., Huntsville, AL.
- Parker, G. R., and D. J. Leopold. 1983. Replacement of *Ulmus americana* L. in a mature east-central Indiana woods. Bulletin of Torrey Botanical Club **110**:482–488.
- Parton, W. J., W. K. Lauenroth, and F. M. Smith. 1981. Water loss from a short-grass steppe. Agricultural Meteorology **24**:97–109.
- Peden, D. G., G. M. Van Dyne, R. W. Rice, and R. M. Hansen. 1974. The trophic ecology of *Bison bison* L. on shortgrass plains. Journal of Applied Ecology **11**:489–498.
- Perryman, L., A. M. Maier, A. L. Hild, and R. A. Olson. 2001. Demographic characteristics of 3 *Artemisia tridentata* Nutt. subspecies. Journal of Range Management **54**:166–170.
- Peterson, G. A., and C. V Cole. 1996. Productivity of Great Plains soils: past, present and future. Pages 325–342 in S. Johnson and A. Bouzaher, editors. Conservation of Great Plains ecosystems: current science, future options. Kluwer Academic Press, Dordrecht, The Netherlands.
- Pflitsch, Andreas, and Julia Ringeis. 2006. Jewel Cave and Wind Cave: A Single Black Hills Cave System? PowerPoint® presentation, Black Hills Area Ecologist and Botanist Workshop, March 9, 2006, Rapid City, SD.
- Plumb, G. E. and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. Ecological Applications **3**:631–643.
- Poff, N. L., M. M. Brinson, and J. W. Day, Jr. 2002. Aquatic ecosystems and global climate change: potential impacts on inland freshwater and coastal wetland ecosystem in the

- United States. Pew Center on Global Climate Change. Online: (http://www.pewtrusts.org/uploadedFiles/wwwpewtrustsorg/Reports/Protecting_ocean_li fe/env_climate_aquaticecosystems.pdf). Accessed 24 April 2009.
- Polley, H. W. and J. K. Detling. 1988. Herbivory tolerance of *Agropyron smithii* populations with different grazing histories. *Oecologia* **77**:261–267.
- Polley, H. W. and J. K. Detling. 1990. Grazing-mediated differentiation in *Agropyron smitthii*: evidence from populations with different grazing histories. *Oikos* **57**:326–332.
- Potvin, M. A., and A. T. Harrison. 1984. Vegetation and litter changes of a Nebraska sandhills prairie protected from grazing. *Journal of Range Management* **37**:55–58
- Primm, S., J. Shay, S. Chaplin, K. Carney, E. Dinerstein P. Sims, A. G. Appleby, R. Usher, K. Kavanagh, M. Sims, and G. Mann. 2001. Northern short grasslands (NA0811). Terrestrial ecoregions. World Wildlife Fund. Online. (http://www.worldwildlife.org/wildworld/profiles/terrestrial/na/na0811_full.html). Accessed 1 May 2007.
- Progulske, D. R. 1974. Yellow ore, yellow hair, yellow pine: a photographic survey of a century of forest ecology. Bulletin 616. Agricultural Experiment Station, South Dakota State University, Brookings.
- Ralston, R. D. 1960. The structure and ecology of the north slope juniper stands of the Little Missouri Badlands. Thesis. University of Utah, Salt Lake City.
- Risser, P. G., E. C. Birney, H. D. Blocker, S. W. May, W. J. Parton, and J. A. Wiens. 1981. The true prairie ecosystem. Hutchinson Ross Publishing Co., Stroudsburg, PA.
- Risser, P. G. 1990. Landscape processes and the vegetation of the North American grassland. Pages 133–146 in S. L. Collins and L. L. Wallace, editors. *Fire in North American tallgrass prairies*. University of Oklahoma Press, Norman, OK.
- Roe, F. G. 1951. *The North American buffalo*. University of Toronto Press, Toronto, Ontario, Canada.
- Romo, J. T. and R. W. Grilz. 2002. Establishment of silver sagebrush in the northern mixed prairie. *Journal of Range Management* **55**:217–221.
- Ruelle, R. 1993. Contaminant evaluation of interior least tern and piping plover eggs from the Missouri River in South Dakota. Pages 159–171 in K. F. Higgins and M. R. Brashier, editors. *Proceedings, the Missouri River and its tributaries: piping plover and least tern symposium/workshop*. South Dakota State University, Brookings.
- Rumble, M. A., L. D. Flake, T. R. Mills and B. L. Dykstra. 2001. Do pine trees in aspen stands increase bird diversity? Pages 185–192 in W. D. Shepperd, D. Binkley, D. L. Bartos, T. J. Stohlgren, and L. G. Eskew, compilers. 2001. *Sustaining aspen in western landscapes: symposium proceedings*; 13-15 June 2000. Grand Junction, CO. Proceedings RMRS-P-18. U. S. Forest Service Rocky Mountain Research Station, Fort Collins, CO.
- Rumble, M. A., and J. E. Gobeille. 1998. Bird community relationships to succession in green ash (*Fraxinus pennsylvanica*) woodlands. *American Midland Naturalist* **140**:372–381.
- Rumble, M. A., and J. E. Gobeille. 2004. Avian use of successional cottonwood (*Populus deltoides*) woodlands along the middle Missouri River. *American Midland Naturalist* **152**:165–177.
- Rumble, M. A., C. H. Sieg, D. W. Uresk, and J. Javersak. 1998. *Native woodlands and birds of South Dakota: past and present*. Research Paper RMRS-RP-8. U. S. Forest Service Rocky Mountain Research Station, Fort Collins, CO.

- Ryerson, D. E., J. E. Taylor, and L.O. Baker. 1970. Clubmoss on Montana rangelands: distribution, control, range relationships. Montana State University Agricultural Experiment Station Bulletin 645.
- Sala, O. E., S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Heunneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**:1770–1774.
- Salas, D. E. and M. J. Pucherelli. 1998*a*. USGS-NPS Vegetation Mapping, Devils Tower National Monument, Wyoming. Computer Data Systems Inc. and Bureau of Reclamation.
- Salas, D. E. and M. J. Pucherelli. 1998*b*. USGS-NPS Vegetation Mapping, Jewel Cave National Monument, South Dakota. Computer Data Systems Inc. and Bureau of Reclamation.
- Salas, D. E. and M. J. Pucherelli. 1998*c*. USGS-NPS Vegetation Mapping, Mount Rushmore National Memorial, South Dakota. Computer Data Systems Inc. and Bureau of Reclamation.
- Salas, D. E. and M. J. Pucherelli. 2003*a*. USGS-NPS Vegetation Mapping, Fort Union Trading Post National Historic Site (Draft Final). Technical Memorandum 8260-02-08, Remote Sensing and GIS Group, Technical Service Center, U.S. Department of the Interior, Bureau of Reclamation, Denver.
- Salas, D. E. and M. J. Pucherelli. 2003*b*. USGS-NPS Vegetation Mapping, Knife River Indian Villages National Historic Site (Draft Final). Technical Memorandum 8260-02-07, Remote Sensing and GIS Group, Technical Service Center, U.S. Department of the Interior, Bureau of Reclamation, Denver.
- Sampson, R. N. 1981. Farmland or wasteland: a time to choose: overcoming the threat to America's farm and food future. Rodale Press, Emmaus, PA.
- Samson, F. B., and F. L. Knopf. 1982. In search of a diversity ethic for wildlife management. *Transactions of the North American Wildlife and Natural Resources Conference* **47**:421–431.
- Sartwell, C. and R. Stevens. 1975. Mountain pine beetle in ponderosa pine: prospects for silvicultural control in second-growth stands. *Journal of Forestry* **73**:136–140.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**:1–15.
- Savage D.A. and L.A. Jacobson. 1935. The killing effect of heat and drought on buffalo grass and blue grama grass at Hays, Kansas. *American Society of Agronomy* **27**:566–582.
- Scher, J. S. 2002. *Juniperus scopulorum*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 23 March 2007.
- Schmiel, D. S., W. J. Parton, F. J. Anderson, R. G. Woodmansee, R. L. Senft, and M. A. Stillwell. 1986. The role of cattle in the volatile loss of nitrogen from the shortgrass steppe. *Biogeochemistry* **2**:39–52.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. *Science* **247**:1043–1048.
- Schwartz, C. C. and J. E. Ellis. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. *Journal of Applied Ecology* **18**:343–353.

- Schwartz, M.W., D. J. Porter, J. M. Randall, and K. E. Lyons. 1996. Impact of nonindigenous plants. Sierra Nevada Ecosystem Project: Final Report to Congress, Volume II, Chapter 47, pages 1203–1226.
- Scott, M. L., A. M. D. Brasher, E. W. Reynolds, A. Caires, and M. E. Miller. 2005. The structure and functioning of riparian and aquatic ecosystems of the Colorado Plateau – Conceptual models to inform monitoring. Draft report to the National Park Service. U.S. Department of Interior, U.S. Geological Survey, Fort Collins, CO.
- Seastedt, T. R. 1988. Mass, nitrogen, and phosphorus dynamics of foliage and root detritus of tallgrass prairie. *Ecology* **69**:59–65.
- Seastedt, T. R., R. A. Ramundo, and D. C. Hayes. 1988. Maximization of soil animals by foliage herbivory: empirical evidence, graphical and conceptual models. *Oikos* **51**:243–248.
- Seastedt, T. R. 1995. Soil systems and nutrient cycles of the North American prairie. Pages 157–176 in A. Joern and K. H. Keeler, editors. *The changing prairie: North American grasslands*. Oxford University Press, New York, NY.
- Shafroth P. B., G. T. Auble, M. L. Scott. 1995. Germination and establishment of the native plains cottonwood (*Populus deltoides* Marshall subsp. *monilifera*) and the exotic Russian-olive (*Elaeagnus angustifolia* L.). *Conservation Biology* **9**:1169–1175.
- Shafroth, P. B., J. R. Cleverly, T. L. Dudley, J. P. Taylor, C. van Riper III, E. P. Weeks, J. N. Stuart. 2005. Control of *Tamarix* in the western United States: implications for water salvage, wildlife use, and riparian restoration. *Environmental Management* **35**:231–246.
- Shepperd, W. D. and M. A. Battaglia. 2002. Ecology, silviculture, and management of Black Hills ponderosa pine. General Technical Report RMRS-GTR-97. U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Shinneman, D. J., and W. L. Baker. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. *Conservation Biology* **11**:1276–1288.
- Sidle, J. G., D. H. Johnson, and B. R. Euliss. 2001. Estimated areal extent of colonies of black-tailed prairie dogs in the northern Great Plains. *Journal of Mammalogy* **82**:928–936.
- Sieg, C. H. 1988. The value of Rocky Mountain juniper (*Juniperus scopulorum*) woodlands in South Dakota as small mammal habitat. Pages 328–332 in R. C. Szaro, and K. E. Severson, editors. *Management of amphibians, reptiles, and small mammals in North America: proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ*. General Technical Report RM-166. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Sieg, C. H. 1991. Rocky Mountain juniper woodlands: Year-round bird habitat on the northern Great Plains. Research Paper RM-296. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Sieg, C. H. 1997. The role of fire in conserving the biological diversity on native rangelands of the Northern Great Plains. Pages 31–38 in D. W. Uresk and G. L. Schenbeck, editors. *Proceedings of the symposium on Conserving Diversity of the Northern Great Plains*. August 17, 1995. Fort Robison State Park, Nebraska. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Sieg, C. H., and H. A. Wright. 1996. The role of prescribed burning in regenerating *Quercus macrocarpa* and associated woody plants in stringer woodlands in the Black Hills of South Dakota. *International Journal of Wildland Fire* **6**:21–29.

- Simms, P.L. 1988. Grasslands. Pages 265–286 in M.G. Barbour and W.D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, New York, NY.
- Simonin, K. 2000a. *Koeleria macrantha*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 13 November 2006.
- Simonin, Kevin A. 2000b. *Euphorbia esula*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 26 April 2006.
- Sims, P. L., and J. S. Singh. 1971. Herbage dynamics and net primary production in certain ungrazed and grazed grasslands in North America. In N. R. French, editor. Preliminary Analysis of Structure and Function in Grasslands. Range Science Department Science Series No. 10. Colorado State University, Fort Collins, CO.
- Stafford Smith, D. M. and S. R. Morton. 1990. A framework for the ecology of arid Australia. *Journal of Arid Environments* **18**:255–278.
- Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife conservation. *Journal of Wildlife Management* **61**:261–270.
- Starfield, A. M., and A. L. Bleloch. 1991. Building models for conservation and wildlife management. Burgess, Edina, MN.
- Steuter, A. A. and H. A. Wright. 1983. Spring burning effects on redberry juniper-mixed grass habitats. *Journal of Range Management* **36**:161–164.
- Stewart, G. and A. C. Hull Jr. 1949. Cheatgrass (*Bromus tectorum* L.)—an ecological intruder in southern Idaho. *Ecology* **30**:58–74.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* **69**:25–46.
- Stohlgren, T. J., K. A. Bull, Y. Otsuki, C. A. Villa, and M. Lee. 1998. Riparian zones as havens for exotic plant species in the central grasslands. *Plant Ecology* **138**:113–125.
- Stromberg J. C., S. J. Lite, R. Marler, C. Paradzick, P. B. Shafroth, D. Shorrock, J. M. White, and M. S. White. 2007. Altered stream-flow regimes and invasive plant species: the *Tamarix* case. *Global Ecology and Biogeography* **16**:381–393.
- Sullivan, J. 1992. *Melilotus officinalis*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 22 March 2007.
- Sullivan, J. 1994. Nebraska sandhills prairie. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Online. (<http://www.fs.fed.us/database/feis/>). Accessed 14 November 2006.
- Sullivan, M. G., L. R. Irby, and C. B. Marlow. 1989. Potential green ash browse in hardwood draws in Theodore Roosevelt National Park. *Prairie Naturalist* **21**:211–217.
- Sullivan, M. G., L. R. Irby, C. B. Marlow, and H. D. Picton. 1988. Distribution, movements, habitat usage, food habits, and associated behavior of reintroduced elk in Theodore Roosevelt National Park. Final report, Contract CX1200-5-A05 1. U.S. Department of the Interior, National Park Service, Denver, CO.
- Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. *Science* **315**:640–642.
- Swengel, A. B. 1996. Effects of fire and hay management on abundance of prairie butterflies. *Biological Conservation* **76**:73–85.

- Swihart, R. K., and N. A. Slade. 1984. Road crossing in *Sigmodon hispidus* and *Microtus ochrogaster*. *Journal of Mammalogy* **65**:357–360.
- Symstad, A. J. 2004. Interim report: Development of the vegetation component of the National Park Service's Northern Great Plains Inventory and Monitoring Network's "Vital Signs" Monitoring Plan. Report for the Northern Great Plains I&M Program, National Park Service, Keystone SD.
Online:(<http://www1.nature.nps.gov/im/units/ngpn/Pages/Monitoring/vegetationSymstad.htm>). Accessed 20 July 2008.
- Symstad, A. J., and M. Bynum. 2007. Conservation of Mount Rushmore National Memorial's Forest. *Natural Areas Journal* **27**:293–301.
- Taylor, J. L. 2001. *Populus deltoids*. Fire Effects Information System. U.S. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Available at <http://www.fs.fed.us/database/feis/>.
- Thorp, J. H., and A. P. Covich. 2001. Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego, CA.
- Thurrow, T. L., W. H. Blackburn, and C. A. Taylor. 1988. Infiltration and interrill erosion responses to selected livestock grazing strategies, Edwards Plateau, Texas. *Journal of Range Management* **41**:296–302.
- Tilman, D., and A. El Haddi. 1992. Drought and biodiversity in grasslands. *Oecologia* **89**:257–264.
- Tobler, M. W., R. Cochard, and P. J. Edwards. 2003. The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania. *Journal of Applied Ecology* **40**:430–444.
- Toomey, R. S., III. 2006. Geological monitoring of caves and associated landscapes. Unpublished report. Mammoth Cave International Center for Science and Learning, Western Kentucky University, Bowling Green.
- Trammell, M. A. and J. L. Butler. 1995. Effects of exotic plants on native ungulate use of habitat. *Journal of Wildlife Management* **59**:808–816.
- Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice: Pattern and process. Springer, New York, NY.
- Uresk, D. W. 1985. Effects of controlling black-tailed prairie dogs on plant production. *Journal of Range Management* **38**:466–468.
- Uresk, D. W. 1987. Effects of livestock grazing and thinning of overstory trees on understory woody plants. Pages 168–171 in F. D. Provenza, J. T. Flinders, and E. D. McArthur, compilers. Proceedings-symposium on plant-herbivore interactions; 1985 August 7-9; Snowbird, UT. GTR-INT-222. U.S. Forest Service, Intermountain Research Station, Ogden, UT.
- Uresk, D. W. 1990. Using multivariate techniques to quantitatively estimate ecological states in a mixed grass prairie. *Journal of Range Management* **43**:282–285.
- Uresk, D. W., and C. E. Boldt. 1986. Effect of cultural treatments on regeneration of native woodlands on the Northern Great Plains. *Prairie Naturalist* **18**:193–201.
- Uresk, D. W., R. M. King, J. Javersak, and T. M. Juntti. 2008. Ecological classification and monitoring. U. S. Forest Service, Washington, D.C. Online.
(<http://www/fs.fed.us/rangelands/ecology/ecologicalclassification/index.shtml>). Accessed 23 March 2009.
- Uresk, D. W., and D. B. Paulson. 1988. Estimated carrying capacity for cattle competing with

- prairie dogs and forage utilization in western South Dakota. Pages 387–390 in Symposium on management of amphibians, reptiles, and small mammals in North America. U.S. Forest Service, Washington, D.C.
- U.S. Fish and Wildlife Service (USFWS). 1993. Pallid sturgeon (*Scaphirhynchus albus*) recovery plan. U.S. Department of Interior, U.S. Fish and Wildlife Service, Bismarck, ND.
- U.S. Forest Service. 2000. Assessment and response to bark beetle outbreaks in the Rocky Mountain area: Report to Congress from Forest Health Protection, Washington Office, Forest Service, U.S. Department of Agriculture. General Technical Report RMRS-GTR-62. U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- U.S. Geological Survey (USGS). 2006. Effects of fire in the northern Great Plains: effects of fire on some undesirable species. USGS Northern Prairie Wildlife Research Center. Online. (<http://www.npwrc.usgs.gov/resource/habitat/fire/undesire.htm>). Accessed 16 February 2007.
- U.S. Geological Survey (USGS). Undated *a*. USGS – NPS Vegetation Mapping Program. USGS. Online. (<http://biology.usgs.gov/npsveg/index.html>). Accessed 14 February 2007.
- U.S. Geological Survey (USGS). Undated *b*. Vegetation descriptions of Agate Fossil Beds National Monument. USGS-NPS Vegetation Mapping Program: Agate Fossil Beds National Monument. Online. (<http://biology.usgs.gov/npsveg/agfo/descript.pdf>). Accessed 13 February 2007.
- U.S. Geological Survey (USGS). Undated *c*. Vegetation description for Fort Laramie National Historic Site. USGS-NPS Vegetation Mapping Program: Fort Laramie National Historic Site. Online. (<http://biology.usgs.gov/npsveg/foia/descript.pdf>). Accessed 14 February 2007.
- U.S. Geological Survey (USGS). Undated *d*. Vegetation descriptions for Scotts Bluff National Monument. USGS-NPS Vegetation Mapping Program: Scotts Bluff National Monument. Online. (<http://biology.usgs.gov/npsveg/scbl/descript.pdf>). Accessed 13 February 2007).
- Van Dyne, G. M., and W. G. Vogel. 1967. Relation of *Selaginella densa* to site, grazing, and climate. *Ecology* **48**:438–444.
- Von Loh, J., D. Cogan, D. Faber-Langendoen, D. Crawford and M. Pucherelli. 1999. USGS-NPS Vegetation Mapping Program, Badlands National Park, South Dakota. Technical Memorandum 8260-00-02, U.S. Bureau of Reclamation Technical Service Center, Denver.
- Von Loh, J., D. Cogan, J. L. Butler, D. Faber-Langendoen, D. Crawford and M. Pucherelli. 2000. USGS-NPS Vegetation Mapping Program, Theodore Roosevelt National Park, North Dakota. U.S. Department of the Interior, Bureau of Reclamation's Remote Sensing and GIS Group, Denver.
- Voorhees, M. E., and D. W. Uresk. 1992. Relating soil chemistry and plant relationships in wooded draws of the northern Great Plains. *Great Basin Naturalist* **52**:35–40.
- Wakimoto, R. H., and E. E. Willard. 2004. Historic fire regimes and change since European settlement on the Northern Mixed Prairie: Effect on ecosystem function and fire behavior. Final Report. Project 98-5-04, Joint Fire Science Program. Boise, ID.
- Walla, J. A., W. R. Jacobi, N. A. Tisserat, M. O. Harrel, J. J. Ball, G. G. Neill, D. A. Reynard, Y. H. Guo, and L. Spiegel. 2000. Condition of green ash, incidence of ash yellows phytoplasmas, and their association in the Great Plains and Rocky Mountain regions of North America. *Plant Diseases* **84**:268–274.

- Walter, H., and H. Lieth. 1960. Klimadiagramm Weltatlas. G. Fischer Verlag, Jena, East Germany.
- Watkinson, A.R. and S. J. Ormerod. 2001. Grasslands, grazing and biodiversity: editors' introduction. *Journal of Applied Ecology* **38**:233–237.
- Weaver, J. E. 1943. Resurvey of grasses, forbs, and underground plant parts at the end of the great drought. *Ecological Monographs* **13**:63–117.
- Weaver, J. E. 1954. North American prairie. Johnsen Publishing Co., Lincoln, NE.
- Weaver, J. E. 1968. Prairie plants and their environment. University of Nebraska Press, Lincoln.
- Webb, C. T., C. P. Brooks, K. L. Gage, and M. F. Antolin. 2006. Classic flea-borne transmission does not drive plague epizootics in prairie dogs. *Proceedings of the National Academy of Sciences of the United States*. **103**:6236–6241.
- Webb, W., S. Szarek, W. Lauenroth, and R. Kinerson. 1978. Primary productivity and water use in native forest, grassland, and desert ecosystems. *Ecology* **59**:1239–1247.
- Wedin, D. A., and D. Tilman. 1992. Nitrogen cycling, plant competition, and the stability of tallgrass prairie. Pages 5–8 *in* D. D. Smith and C. A. Jacobs, editors. *Proceedings of the twelfth North American prairie conference*. Cedar Falls, IA.
- Welch, B. A. 2007. The plant invasion process: implications for land managers. Chapter 2 *in* P. H. Geissler and B. A. Welch, editors. *Early detection of invasive plants: A handbook* [Draft April 27, 2007]. United States Department of Interior. Online. (<http://www.pwrc.usgs.gov/brd/invasiveHandbook.cfm>) Accessed 10 May 2007.
- Welch, B. L. and Criddle, C. 2003. Countering misinformation concerning big sagebrush. Research Paper RMRS-RP-40. U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Wendtland, K. J., and J. L. Dodd. 1992. The fire history of Scotts Bluff National Monument. Pages 141–143 *in* D. D. Smith and C. A. Jacobs, editors. *Proceedings of the twelfth North American prairie conference*. Cedar Falls, IA.
- West, N. E. and T. P. Yorks. 2002. Vegetation responses following wildfire on grazed and ungrazed sagebrush semi-desert. *Journal of Range Management* **55**:171–181.
- West, N. E., and J. A. Young. 2000. Intermountain valleys and lower mountain slopes. Pages 255–284 *in* M. A. Barbour and W. D. Billings, editors. *North American terrestrial vegetation*. Second edition. Cambridge University Press, New York, NY.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* **42**:266–274.
- Whicker, A. D. and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. *BioScience* **38**:778–785.
- Whisenant, S. G., and D. W. Uresk 1990. Spring burning Japanese brome in a western wheatgrass community. *Journal of Range Management* **43**:205–208.
- White, E. M., and J. K. Lewis. 1967. Recent gully formation in prairie areas of the Norther Great Plains. *Plains Anthropologist* **12**:318–322.
- White, R. S., and P. O. Currie. 1983. The effects of prescribed burning on silver sagebrush. *Journal of Range Management* **36**:611–613.
- Whitford, W. G. 1986. Decomposition and nutrient cycling in deserts. Pages 93–117 *in* W. G. Whitford, editor. *Pattern and process in desert ecosystems*. University of New Mexico Press, Albuquerque.
- Wilhite, D. A. and R. O. Hoffman. 1979. Drought in the Great Plains: A bibliography. Institute of Agriculture and Natural Resources, University of Nebraska, Lincoln.

- Wolters, G. L., C. H. Sieg, A. J. Bjugstad, and F. R. Gartner. 1994. Herbicide and fire effects on leafy spurge density and seed germination. Research Note RM-526. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Woodruff, L.W., W. F. Cannon, and C.L. Dicken. 2002. Impact of fire on the geochemistry of the forest floor and mineral soils, north-central U.S.: Poster. Online. (http://firescience.cr.usgs.gov/slides/woodruff_geochemsoils2.pdf). Accessed 24 May 2009.
- Yeaton, R. I. and K. J. Esler. 1990. The dynamics of a succulent Karoo vegetation: a study of species association and recruitment. *Vegetatio* **88**:103–113.
- Zavaleta, E. 2000. The economic value of controlling an invasive shrub. *Ambio* **29**:462–467.
- Zimmerman, G. M. 1981. Effects of fire upon selected plant communities in the Little Missouri Badlands. Thesis. North Dakota State University, Fargo.